THE ECOLOGICAL ROLE OF BRYOPHYTES IN ALPINE STREAMS OF NEW ZEALAND

A thesis

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"Mosses are useful to the insect tribe, countless numbers of which find homes among their branches, and roam about in their shades as in mighty forests, looking with their thousand eyes upon the wonders of their leaves, and sunning their wings of purple and gold, and burnishing their shining armour upon the polished columns of their urns."

Frances Tripp, British Mosses, 1888. (In: Gerson 1972)

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PREFACE: A PERSONAL INTRODUCTION.

The last four and a half years for me have been interesting, and full of both stimulating moments and overwhelming monotony of sample sorting. I have realised that being a PhD student is in many ways like mountain climbing, where in essence one sets about achieving a simplistic, predefined goal. Some of the rewards of these are also similar: unobstructed views of glaciers and cloud filled valleys, or a series of connected points along a graph. Both are simple to behold, yet both belie the effort to obtain. Both are also rather transient and abstract achievements: a peak; a finished thesis. What follows on, however, is important.

As people who climb mountains are often asked, I too was also asked why I put up with the life of a research student. The "science" intrigues me, but is certainly not the most important aspect. The feeling of discovery, of doing what no-one else has done before also appeals to me. If the days of being a geographical explorer are gone, I find that even in the twentieth century there are many ways each one of us can explore the wonder and beauty of Nature, and tread untrodden passages.

I feel however that the most important thing that this study has taught me is to question my role as a biologist in society. Aldo Leopold's "**A Sand County Almanac**" portrays an alarming picture of university professors, sitting in their ivory towers while coldly dismembering and describing the "instruments of the great orchestra". But although they are constantly plucking the strings of their own instruments, they do not listen to the music,

> "For all are restrained by an ironbound taboo which decrees
> that the construction of instruments is the domain of science,
> while the detection of harmony is the domain of poets".

Although the great thing about science is its objectivity, this is sometimes a hindrance. As scientists, we are constrained to facts, and we are allowed no place in scientific writing for our emotions and personal beliefs. Yet it is largely this unspoken component that plays such a major part in determining our research efforts: indeed most of my research was spurred on by my love of alpine environments and small, unnoticed plants and animals.

But I feel that there is more to it than this, and that as biologists we should perhaps attempt to not only listen to the "music" of Nature, but also to protect it from being destroyed by our so-called march of progress. Aldo Leopold succinctly summed up what has been one of my greatest fears about this cold process of dismemberment, i.e., research:

> "Let no man jump to the conclusion that Babbit must take his PhD in ecology before he can see his country. On the contrary, the PhD may become as callous as an undertaker to the mysteries at which he officiates."

While tramping in some of New Zealand's many temperate rainforests, I have always been struck at the amazing beauty of the trees, forest floor, and of course streams, with their profuse bryophyte growths, and have often wondered whether I see them differently to non-biologists. Even if I do, I hope I never tire of their beauty, and cease to become enchanted by them. If I have to remain like Antoine Saint Exupery's "Little Prince" to achieve this, then so be it. And like his naive little character, I always have to remind myself that surely ours is the one profession where we have a moral obligation to preserve the things we study, and not be content with merely classifying each instrument before it is broken in the rush of progress.

I think this is best summed up in the words of the great American limnologist, Evelyn Hutchinson:

> "The writer believes that the most practical lasting benefit science can now offer is to teach man how to avoid destruction of his own environment, and how, by understanding himself with true humility and pride, to find ways to avoid injuries that at present he inflicts on himself with such devastating energy." *American Scientist* (1943)

What was true in 1943 is certainly true today, and I hope that my training can help me achieve this worthwhile goal.

Alastair Suren

(November 1990)

ABSTRACT

The ecological roles of aquatic bryophytes in 2 small New Zealand alpine streams were investigated. The streams differed with respect to algal biomass and detrital inputs, reflecting their location either above the tree-line (Mouse Stream) or flowing through mountain beech forest (Tim's Creek). Streambed instability was also higher in the forested site.

Quantitative sampling of bryophytes and riffles over 18 months revealed the existence of discrete macroinvertebrate (>250 μm) and meiofaunal (i.e., <250μm) communities within bryophytes. Here, macroinvertebrate and meiofaunal densities in bryophytes were up to 10, and 24 times greater than in riffles at Mouse Stream, and up to 7, and 15 times greater at Tim's Creek.

Faunas colonizing non-edible bryophyte analogues were similar to those colonising real plants, suggesting that invertebrates colonise these plants for their non-trophic properties. Manipulations of artificial bryophytes altered quantities of potential food (i.e., periphyton and detritus) and degree of shelter (i.e., "stem" density) to ascertain the importance of these in regulating invertebrate colonization. Functional responses to these variables differed between species and between sites. Positive relationships existed between invertebrate density and algal and detrital biomass, and shelter at Mouse Stream; the trends at Tim's Creek were not as evident and were masked by increased streambed instability and flooding.

Assessment of bryophyte consumption by gut content analysis revealed that only three of 23 taxa examined contained >5% of bryophyte material in their guts. The cranefly *Limonia hudsoni* was the only taxa that appeared to graze bryophytes extensively. Lack of consumption may be related to that fact that bryophytes contained more refractory, and less "digestible" material than selected riparian vegetation, or to the presence of antiherbivore compounds within some species.

The importance of bryophytes in affecting energy inputs into streams was finally examined. Algal biomass was higher on structures mimicking bryophytes than stones, and biomass was higher above the tree-line than below. Natural bryophytes trapped more FPOM than riffles, and mimics at Tim's Creek trapped more FPOM than at Mouse Stream. Bryophyte biomass at both sites however was similar, reflecting the ability of these plants to tolerate a wide range of light regimes. Retention of introduced organic matter into streams was influenced by bryophytes, whereby streams with these plants retained material better than streams without.

CHAPTER ONE:

GENERAL INTRODUCTION

INTRODUCTION

New Zealand alpine streams

A dominant feature of New Zealand's South Island is the Alpine Fault, where the Indo-Australian and Pacific tectonic plates are slowly sliding past each other. Over the last two million years lateral displacement of this fault has been approximately 480 km, and vertical uplift has raised the rocks of the Southern Alps by nearly 18 000 m (Chinn 1986a). Despite this enormous uplift of the earth's crust, the maximum height of the Southern Alps is only 3764 m, at Mt. Cook. Further north in Arthur's Pass National Park, the site of my research, peaks rise to between 1600 and 2400 m (Mt. Murchison). Here, as elsewhere in the Alps, warm, moisture laden air is frequently forced over the mountains by strong north-west winds, and the moisture is released as snow and rain. Total annual precipitation at Arthur's Pass National Park Headquarters, east of the Main Divide, averages 5-7 m and is even higher west of the divide at Otira (Chinn, 1986b). High winds, rainfall and extensive glaciation during the Pleistocene epoch have eroded the mountains as quickly as they have grown. The resultant topography of Arthur's Pass National Park is one of a heavily eroded mountain landscape, characterised by large, unstable screes, U-shaped glaciated valley systems, hanging waterfalls, gorges, chasms and rocky bluffs.

Within the Park exist an abundance of watercourses; permanent springs, glacial and tarn fed streams, and temporary conduits that carry away flood waters during high rainfall or summer snow melt. The substratum of these streams consists primarily of shattered greywacke, argillite and schist, fragments of which are constantly being transported downstream and further weathered and broken. Substratum movement is often extensive, and organic material is continually being washed downstream during frequent flooding. Populations of algae that develop on the more stable boulders are also strongly influenced by discharge, with physical abrasion from the water and suspended sediments mitigating against the development of high biomass.

Aquatic bryophytes

One result of the steep topography, extensive channel erosion, and highly variable discharge of alpine streams is that loose materials are constantly being moved from fast flowing and steep erosional areas. Consequently, large areas of bedrock are often exposed, either at waterfalls or in narrow chasms and chutes where discharge of water is often high. These bedrock areas are frequently colonised by aquatic bryophytes, which can form deep and extensive mats.

Studies of distantly related bryophyte families have led to the theory that rheophilous species have evolved along parallel lines from terrestrial stocks (Vitt & Glime 1984). Aquatic bryophytes characteristically have stiff wiry stems, are dark coloured, have small thick-walled leaf cells and are strongly attached to the substratum (Odu 1978, Glime *et al.* 1979, Geissler 1982, Vitt & Glime 1984). These traits have enabled bryophytes to grow abundantly in bedrock habitats and to cope with the environmental stresses inherent in this environment. These include high current velocities, potentially great abrasion damage from waterborne particles, sediment build up between shoots, almost constant inundation and often cold temperatures.

Unlike their xeric counterparts, aquatic bryophytes cannot withstand desiccation (e.g., Fornwall & Glime 1971, Glime 1971). This is not because they lose moisture more quickly than terrestrial bryophytes (Krocho *et al.* 1978) but because they are not physiologically adapted to cope with this kind of stress. When aquatic mosses dry out, many irreversible cellular changes occur; e.g., ribosomal systems disintegrate (Krupa 1977); ATP may be lost from cells disrupting protein synthesis (Bewley & Gwodz 1975); and membrane disruption around chloroplasts, mitochondria and thylakoids (Krochko *et al.* 1978) causes extensive cellular damage. Their low desiccation resistance may also explain the presence of bryophyte zones that correlate closely with inundation regimes and height above water (Tutin 1949, Gimingham & Birse 1957, Glime 1970, Craw 1976, Cowie & Winterbourn 1979, Vitt & Glime 1984, Slack & Glime 1985).

Temperature stress experienced by fully aquatic bryophytes is generally low because the temperature regimes encountered in most freshwaters are relatively

narrow and predictable. Aquatic bryophytes typically have lower temperature optima than their terrestrial counterparts (Dilkes & Proctor 1975), and these usually reflect ambient environmental conditions (Fornwall 1978, Fornwall & Glime 1982). However, aquatic bryophytes can face temperature extremes. Very low temperatures are usually of little consequence to their survival as leaf cells effectively become insulated from extremely cold external temperatures when the surrounding water freezes (Glime & Vitt 1984). On the other hand, high summer temperatures can be detrimental, and may be responsible for the greatly reduced aquatic bryophyte diversity found in tropical regions (Vitt & Glime 1984).

Effects of abrasion by waterborne particles on bryophyte growth may be considerable. For example increased water velocity (and therefore abrasion) resulted in greatly reduced proportions of leafy to bare stems in the moss *Fontinalis novae-angliae* Sull. because of leaf loss from lower (and older) sections of stem (Conboy & Glime 1971). Abrasion is also thought to at least partially explain the observed distributional patterns of *Plagiochila* and *Fontinalis* in a New Hampshire stream (Glime 1970) and of bryophyte communities in a New Zealand stream (Craw 1976).

Nevertheless, despite having to contend with physical stresses in headwater streams, it is clear that bryophytes have successfully exploited this niche. Most ecological studies on aquatic bryophyte distributions have been made in North America (e.g., Glime 1968a,b, Glime 1970, Slack & Glime 1985, Sheath *et al.* 1986), but others have been made in Ireland and Wales (Frost 1942, 1945, Ormerod 1987), New Zealand (Craw 1976, Cowie & Winterbourn 1979), France (Dawson 1973) and the Western Himalayas (Pant & Tewin 1984). All these studies illustrate the success of this plant group in low-order, turbulent streams.

Invertebrate communities

The alpine stream environment has also had an important influence on invertebrate community structure in New Zealand in terms of species composition, distribution, and abundance. Although alpine stream faunas have presumably evolved in an environment typified by unpredictable and fluctuating discharge, high substrate

movement and low abundance of algae and detritus biomass, the fauna often shows reductions in taxonomic richness or density in unstable streams (Rounick & Winterbourn 1983, Collier & Winterbourn 1987, Graesser 1988). Many of the insects in mountain streams have asynchronous, multivoltine life histories (Cowie 1980) and are known to graze extensively on persistent stone surface organic layers (epilithon) and associated fine particulate organic matter (Cowie 1980, Rounick & Winterbourn 1983, Winterbourn 1986). Faunas are typically dominated by a core assemblage of such organic-layer browsers and fine particle collectors (Winterbourn 1986) whose populations are resilient in the face of physical disturbances (Winterbourn and Rounick 1985, Graesser 1988).

Rationale for the present study

The combination of predominantly unstable riffles interspersed with stable bedrock, waterfalls and chutes colonized extensively by bryophytes represent extreme ends of an environmental stability continuum that stream invertebrates encounter in alpine streams. It seems probable that animals living among bryophytes experience less environmental perturbations than those colonizing unstable riffles, and may consequently have formed specific associations with these plants. The primary aim of mine was to determine whether this was so in streams of Arthur's Pass National Park. Intensive studies were made in two streams, one above and one below the tree-line, to compare the interactions between invertebrates and bryophytes and determine whether any differences may be a consequence of contrasting riparian settings.

Comparisons of animal communities in bryophyte and stony riffles were made to determine if bryophytes enhanced invertebrate densities and whether differences in species composition existed between these two habitats. I initially considered only those invertebrates that were trapped by 250 µm mesh sieves (Chapter 2). This study served as the baseline for future work, and answered the fundamental question as to which stream invertebrates lived where. I also began to formulate further questions about bryophyte-animal interactions during this phase of the study.

Broadening of the study to include meiofauna (i.e., tardigrades, nematodes, rotifers and copepods) was stimulated largely by the realisation that they are often very

abundant in both Antarctic aquatic environments (Suren 1990), and my study streams. Because of the sieve size used during sample processing, most of the meiofauna was not considered in the initial field program (Chapter 2), so it was completed with an investigation that focussed specifically on this group (Chapter 3).

Having established that bryophytes supported discrete invertebrate assemblages, the next phase concerned potential reasons for this. Initial field experiments showed that artificial substrates mimicking bryophytes were colonized by a similar fauna to that associated with living bryophytes (Chapter 4). A subsequent series of experiments tested reasons for invertebrate colonization of bryophytes. The importance of shelter, periphyton biomass, and the accumulation of detritus was examined by manipulating artificial substrata at my two study sites with respect to these factors (Chapter 5).

The extent of bryophagy in each stream was investigated. Differences in invertebrate diets were compared not only between riffles and bryophytes, but also between animals collected from above, and below the tree-line. This was done to determine if bryophytes in each stream might be subject to different grazing pressures if alternative food resources differed in availability (Chapter 6). In addition, the food values of bryophytes and selected riparian plants were compared.

The net productivity of periphytic algae associated with grass carpet covered tiles (representing bryophytes) and bare tiles (representing unenclosed riffles), and the temporal dynamics of detritus associated with these substrata was examined over a period of 23 months (Chapter 7). In addition, the biomass of living bryophytes, and that of organic matter trapped within bryophytes and riffles was measured at each site (in association with the invertebrate study described in Chapter 2).

Previous work on New Zealand mountain streams has highlighted the importance of stone surface organic layers as sites of carbon transfer to consumers and illustrated the poor capacity of many streams to retain coarse allochthonous organic matter (Rounick 1982, Winterbourn 1986, Graesser 1988). The effects of bryophytes on organic matter retention in various streams was investigated further in this study (Chapter 8).

Most of the chapters in this thesis are written in the form of scientific papers (excluding abstracts and redundant study site descriptions) and one consequence of

this is that some repetition of material covered in the Introduction and Discussion sections has been unavoidable. The final section (Chapter 9) is a theoretical discussion of my findings, and considers how they relate to our present knowledge of the ecological role of bryophytes in stream ecosystems.

CHAPTER TWO:

THE INVERTEBRATE FAUNA OF AQUATIC BRYOPHYTES

IN TWO CONTRASTING ALPINE STREAMS OF NEW ZEALAND

INTRODUCTION

New Zealand mountain streams typically flow through steep, finely dissected mountain catchments that are often above the tree-line and experience heavy and unpredictable rainfall (Winterbourn 1978). In such streams, organic matter retention is presumed to be low (Graesser 1988) and the fauna is dominated by a core assemblage of collectors and browsers (Cowie 1980, Winterbourn *et al.* 1981, Graesser 1988). Shredders are rare or absent (Rounick & Winterbourn 1982). Some surveys have shown that invertebrate densities and/or taxonomic richness can be negatively correlated with channel substratum instability (Towns 1979, Cowie 1980, Rounick & Winterbourn 1983, Collier and Winterbourn 1987, Graesser 1988) and therefore it has been inferred that this plays a major role in structuring invertebrate communities (Collier 1988, Graesser 1988).

Nevertheless, stable surfaces such as bedrock and very large boulders do occur in some "unstable" headwater streams. These are often colonised by luxuriant growths of aquatic bryophytes. Substratum stability appears to be of major importance in controlling bryophyte growths in streams (Sheath *et al.* 1986), and of course it has long been known that "the rolling stone never gathereth moss" (Heywood 1362).

Aquatic bryophytes can occur as mats or wefts (*sensu* Gimingham & Birse 1957). Both growth forms minimise water drag and maximise the surface area in contact with the substratum thereby enabling bryophytes to grow at high current velocities (Vitt & Glime 1984). Their presence greatly increases spatial heterogeneity of otherwise homogeneous bedrock faces, reduces current flows within their matrices and greatly increases the surface area available for colonization by invertebrates.

In numerous studies it has been found that the densities of invertebrates are greater on bryophytes than in stony riffles (e.g., Thienemann 1912, Carpenter 1927, Percival & Whitehead 1929, 1930, Frost 1942, 1945, Lillehammer 1966, McElhone & Davies 1985, McKenzie-Smith 1987, Brusven *et al.* 1990), although species richness in each habitat is often comparable (Hynes 1961, Egglishaw 1969, Thorup & Lindegaard 1977). Frequently, many more early instars of insects occur among bryophytes than in stony riffles (Hynes 1961, Egglishaw 1969, Thorup & Lindegaard 1977, McKenzie-Smith 1987),

either because of selective oviposition by adults, enhanced survival within this habitat, or selective migration of smaller individuals into, and larger individuals away from bryophytes (Byers 1961, Gerson 1972). Bryophytes also provide unsuitable habitat for some molluscs and large, dorso-ventrally flattened ephemeropterans (Percival & Whitehead 1929, 1930, Lillehammer 1966), which may be unable to move freely through densely packed bryophyte stems.

Except for a study of the invertebrate fauna in mosses of a sub-alpine springbrook at Cass (Cowie 1975, Cowie & Winterbourn 1979), there have been no investigations of invertebrate assemblages associated with bryophytes in New Zealand streams. I therefore undertook the present study in two contrasting South Island alpine streams to determine whether distinct invertebrate communities were associated with bryophytes, and whether taxa were consistently found in this habitat above and below the tree-line.

STUDY SITES

The two study streams were 3 km. apart and situated north of Arthur's Pass village where meteorological records were obtained (Fig. 1). Average monthly air temperatures ranged from -2.3°C in July to 16.6°C in January. Annual rainfall exceeded 4000 mm and was seasonally unpredictable (Fig. 2). Snow covered the ground around Mouse Stream on sampling occasions in July, August and October 1986, and during July and August 1987. Snow was only present around Tim's Creek once, in July 1986.

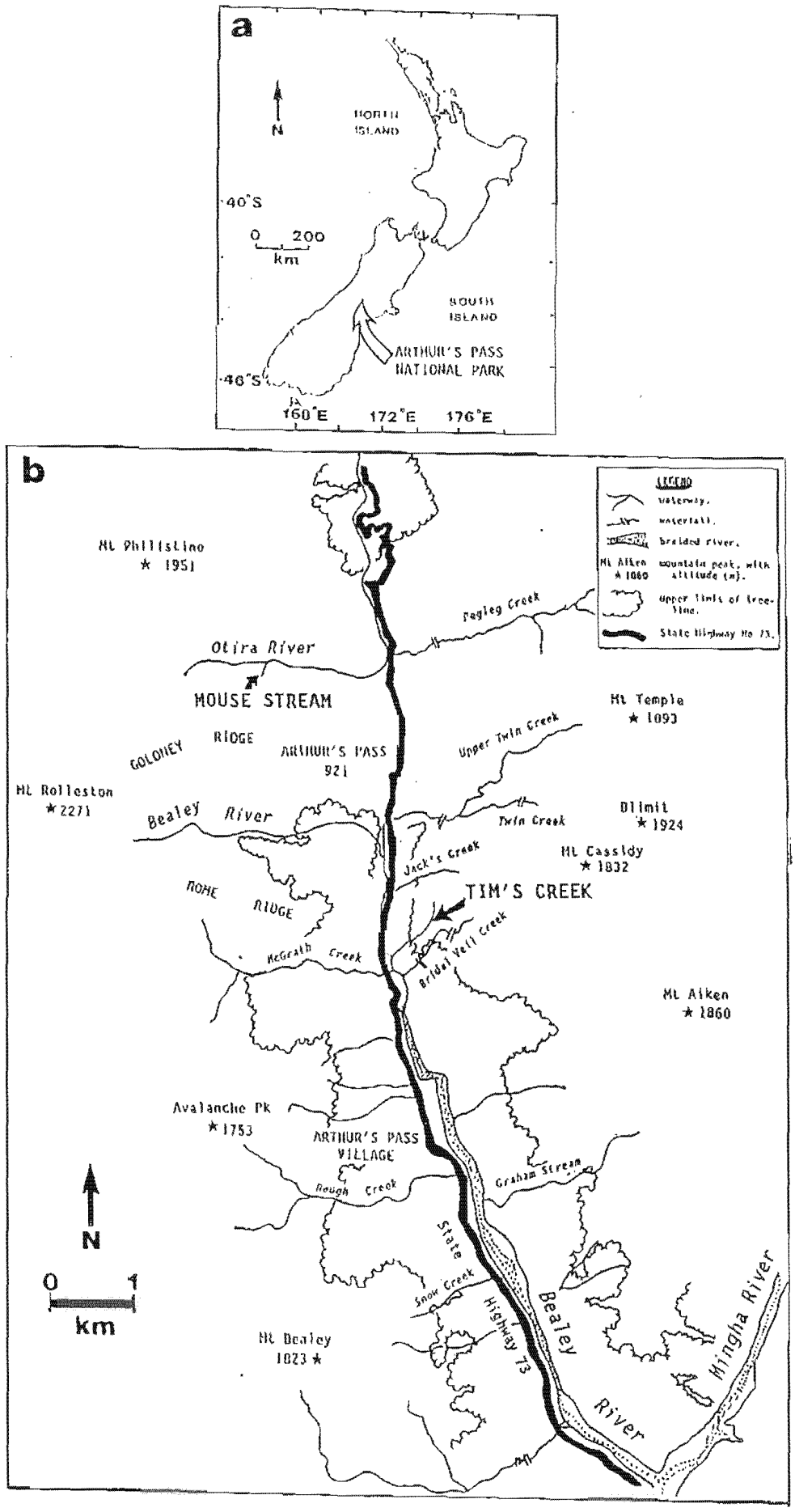


Fig. 1: Location of Arthur's Pass National Park in approximately the centre of the South Island, about 150 km from Christchurch (a). Within the Park I chose 2 small streams as study sites. "Mouse Stream" is located in the Otira Valley above the tree-line, and Tim's Creek flows through mountain beech forest on the lower slopes of Mt. Cassidy (b).

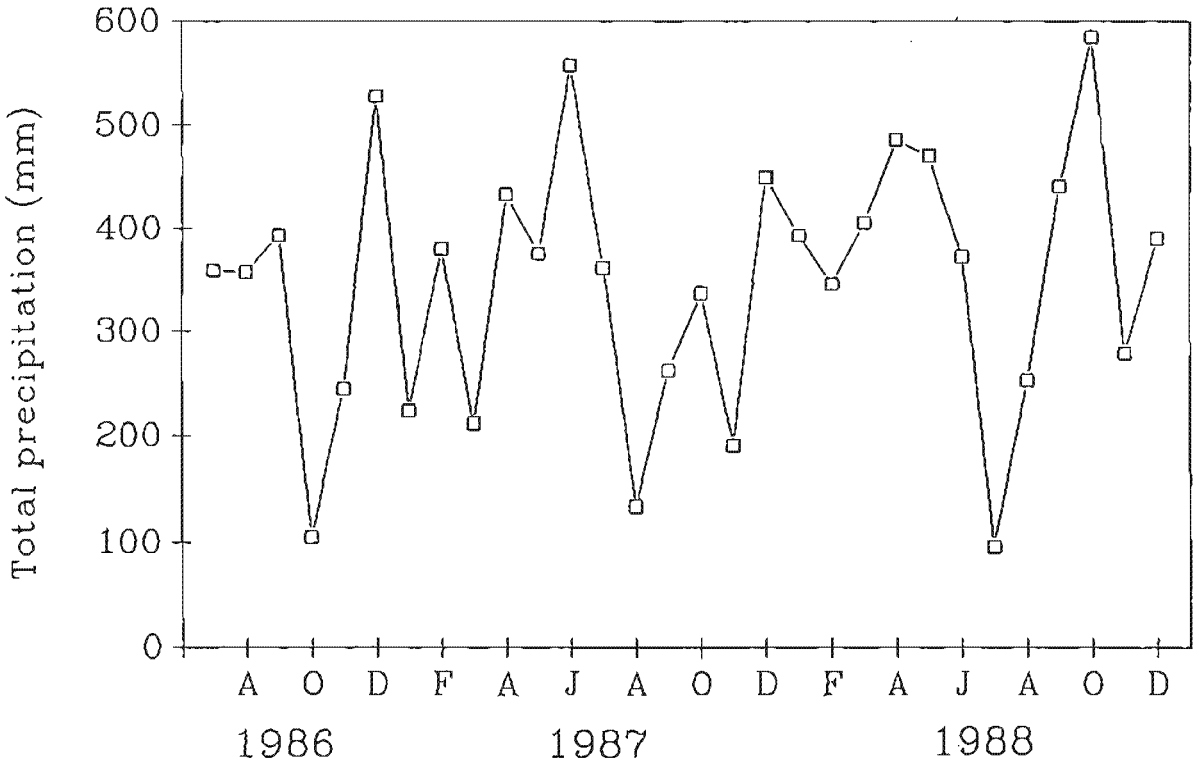


Fig. 2: Total monthly precipitation recorded at Arthur's Pass Village from July 1986 to December 1988 showing lack of a defined seasonal pattern.

Mouse Stream

"Mouse Stream", is a small (1-2 m wide) spring fed tributary of the Otira River with its origin on the lower slopes of Goldney Ridge at approximately 1100 m (Figs 1, 3). Catchment vegetation consisted of tall tussock grassland and associated alpine shrubs. The narrow (*ca.* 50-75 cm) upper reaches of Mouse Stream flowed beneath dense, overhanging vegetation dominated by alpine tussock (*Chionochloa pallens* Zotov and *C. flavescens* Zotov), and mountain hebes (*Hebe subalpina* (Ckn.) Ckn. *et al.* and *H. odora* (Hook.f.)Ckn), and with various other plants growing adjacent to, and hanging into the water (Table 1). In its lower reaches, the stream was wider (<2 m) and not shaded by riparian plants.

Although the upper part dried up or froze during some winter months, the lower 30 m flowed continuously and was where sampling was conducted. The stream channel consisted of a mixture of large boulders and bedrock falls (25-75 cm high) separating stony riffles. These had substrata of coarse angular cobbles (<15 cm diameter) overlying small gravel (< 3 cm) and silt. Water velocity was low (*ca* 0.32 m s^{-1}) and fairly constant throughout the year reflecting the spring source, although high discharges in lower reaches were noted during times of heavy rainfall. Streambed stability was assessed with the streambed component of the Pfankuch (1975) procedure, modified slightly for use in these first order streams (Table 2), and was rated as "high" (score = 23).

Dominant bryophytes within the stream channel were the mosses *Fissidens rigidulus* Hooke.f. & Wils., *Cratoneuropsis relaxa* (Hooke.f. & Wils.) Fleisch. in Broth., and *Bryum blandum* Hooke.f. & Wils.. These were restricted to bedrock and larger boulders in the lower half of the stream, whereas upstream close to the source bryophytes grew over smaller cobbles and gravel.

Periphyton growth was often extensive, and commonly covered bryophytes, decaying riparian vegetation and stones in riffle areas. The periphyton was dominated by flocculent masses of the filamentous diatom *Diatoma hiemale* var *mesodon* (Ehr) Grun. that extensively covered both stones and bryophytes. Other species of algae, including various pennate diatoms (e.g., *Navicula, Cymbella* and *Synedra*), the

Table 1: Taxonomic list of common riparian vegetation growing close to the study sites.

MOUSE STREAM	TIM'S CREEK
Acaena anserinifolia (J.R. Druce et C. Forst)	**Acaena* spp.
Celmisia semicordata Petrie	*Astelia nervosa* Banks & Sol. ex Hook.f.
Chionochloa flavescens Zotov	**Blechnum capence* (L.) Schlecht.
**C. pallens* Zotov	*Celmisia glandulosa* Hook. f.
**Coprosma serrulata* Hook. f. ex Buchan.	*Chionochloa conspicua* Zotov
**Gaultheria crassa* Allan	*Coprosma foetidissima* J.R. et G Forst
Gingidia montana (J.R. & G Forst.) Dawson	*C. pesudocuneata* W.R.B. Oliver
Hebe odora (Hook.f.) Ckn	*Coprosma* spp.
**H. subalpina* (Ckn.) Ckn. et al.	*Dracophyllum longifolium* (J.R. & G Forst) R.Br.
Helichrysum bellidioides (Forst. f.) Willd	**D. traversii* Hook.f.
Marsipposperrnum gracile (Hook .f.) Buch.	*Gaultheria antipoda* Forst.f.
**Ranunculus lyalli* Hook f.	*Gingidia montana* (J.R. & G. Forst.) Dawson
	**Marsipposperrnum gracile* (Hook. f.) Buch.
	**Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole
	Olearia arborescens (Forst.f.) Ckn. et. Laing
	Phyllocladus alpinus Hook.f.
	Phormium cookianum Le Jolis
	Podocarpus nivalis Hook.
	Pseudopanax colensoi Hook. f

*Species commonly seen to contribute to allochthonous inputs to each stream.

Table 2: Modified Pfankuch channel stability evaluation form (after Rounick & Winterbourn 1982) for use in first order alpine streams. The zones relating to upper and lower banks are not included. Epilithon development (either algae or amorphous "organic slimes" on rocks) has been included as a new category, "c", as it was observed to be related to stream discharge and substrate stability. Item "d" of Rounick & Winterbourn (1982) has been divided into two categories: bottom size distribution, "e", and percentage stable materials " f". Individual Pfankuch rating scores for each item are given for each category. Total scores are obtained by summing scores for individual items; a high score is indicative of low channel stability.

ITEM RATED STREAM BED	Stability Indicators by Classes Excellent	Good	Fair	Poor
a Shape and angularity of rocks	Sharp edges/corners Rough surfaces 1	Rounded corners & edges; smooth/flat surfaces 2	Corners & edges well rounded in 2 dimensions 3	Well rounded in all dimensions; surfaces smooth 4
b Rock brightness (smooth)	Surfaces dull or stained; generally not bright 1	Mostly dull; up to 35% bright 2	Mixture; 50% dull, 50% bright 3	Mostly bright; > 65% 4
c Epilithon development	Surfaces of large boulders and cobbles very slippery and dark 1	Surfaces of only large stable boulders slippery and dark 2	Surfaces of large boulders > 50% covered by epilithon; layer usually thin. 3	No visible epilithon present, rocks not slippery 4
d Packing of substrate material	Assorted sizes tightly packed 2	Moderately packed 4	Mostly a loose arrangement 6	No packing evident; loose easily moved assortment. 8
e Size and distribution of materials	No change in sizes evident 2	Size distribution shift slight 4	Moderate distribution change 6	Marked distribution change 8
f Percentage of stable substrate	Stable materials 80-100%; bedrock often evident 2	Stable materials 50-80%; bedrock usually evident 4	Stable materials 20-50%; bedrock areas rarely exposed in stream. 6	Stable materials 0-20%; exposed bedrock areas not present. 8
g Evidence of scouring and deposition	<5% of bottom & banks affected 6	5-30% of bottom and banks, usually where gradients steepen. 12	30-50% affected scouring evident at constrictions, bends and obstructions. 18	>50% of stream land in a state of flux; banks partly defined and eroding 24
h Presence of aquatic plants	Abundant bryophyte and algal growths 1	Common; bryophytes particularly distributed on larger boulders; algae often common. 2	Present but a bit spotty, bryophytes rare and algae a thin crust. 3	Perennial types scarce or absent bryophytes absent, algae not very visible. 4

Fig. 3: View of Mouse Stream, Upper Otira Valley, showing the lower portion of the stream immediately above its confluence with the Otira River. Bryophytes occurred only on large, immobile boulders and bedrock. Riffles consisted of small gravel and cobbles with occasional large rocks. Riparian vegetation was dominated by tussock and small shrubs; e.g., *Hebe* spp.

cyanobacteria *Lyngbya, Chamaesiphon, Tolypothrix* and *?Placoma,* filamentous green algae *Ulothrix zonata* (Weber & Mohr) Kutz., and *Tetraspora* were also occasionally common on rocks and bryophytes.

Tim's Creek

"Tim's Creek", is a larger, (1-3 m wide) spring-fed tributary of the Bealey River, with its source on the lower slopes of Mt. Cassidy at approximately 900 m (Figs 1, 4). Sampling was restricted to a 200 m reach some 500 m below the source. The stream channel consisted of deep pools (up to 1 m deep) and shallow stony riffles (<20 cm deep) separated by bedrock falls and chutes. Although the stream channel was well defined, stream discharge was highly variable and gravel substrata moved extensively during high flows. This was exemplified by the sudden collapse of a large debris jam (a buried beech tree log) which resulted in the loss of much gravel and cobble substrata from the immediate area. This great physical instability was reflected in the larger Pfankuch score (34).

Riparian vegetation was dominated by a continuous canopy of mountain beech (*Nothofagus solandri* var *cliffortioides* (Hook.f.)Poole) beneath which the shrub subcanopy was dominated by *Dracophyllum traversii* Hook.f. Riparian understorey plants grew to the stream's edge and consisted of mixtures of tussock grasses, reeds, shrubs, herbs and ferns (Table 1).

Bryophytes were particularly common in chutes and included the liverworts *Plagiochila retrospectans* Nees, *Hepatostolonophora paucistipula* (Rodway) Engel, *Lophocolea planiscula* (Hook.f.& Taylor) Taylor ex Gottsche *et al.* the hornwort *Anthoceros laevis* L., and the mosses *F. rigidulus* and *Pterygophyllum dentatum* (Hooke.f. & Wils.) Dix.

Periphyton was far less obvious than at Mouse Stream, and was composed primarily of a thin, black crust that coated stone surfaces. This was dominated by the encrusting diatom *Epithemia sorex* Kutz. although cyanobacteria (e.g., *Lyngbya, Tolypothrix* and *Chamaesiphon*) and the pennate diatoms *Diatoma* and *Synedra* were locally abundant.

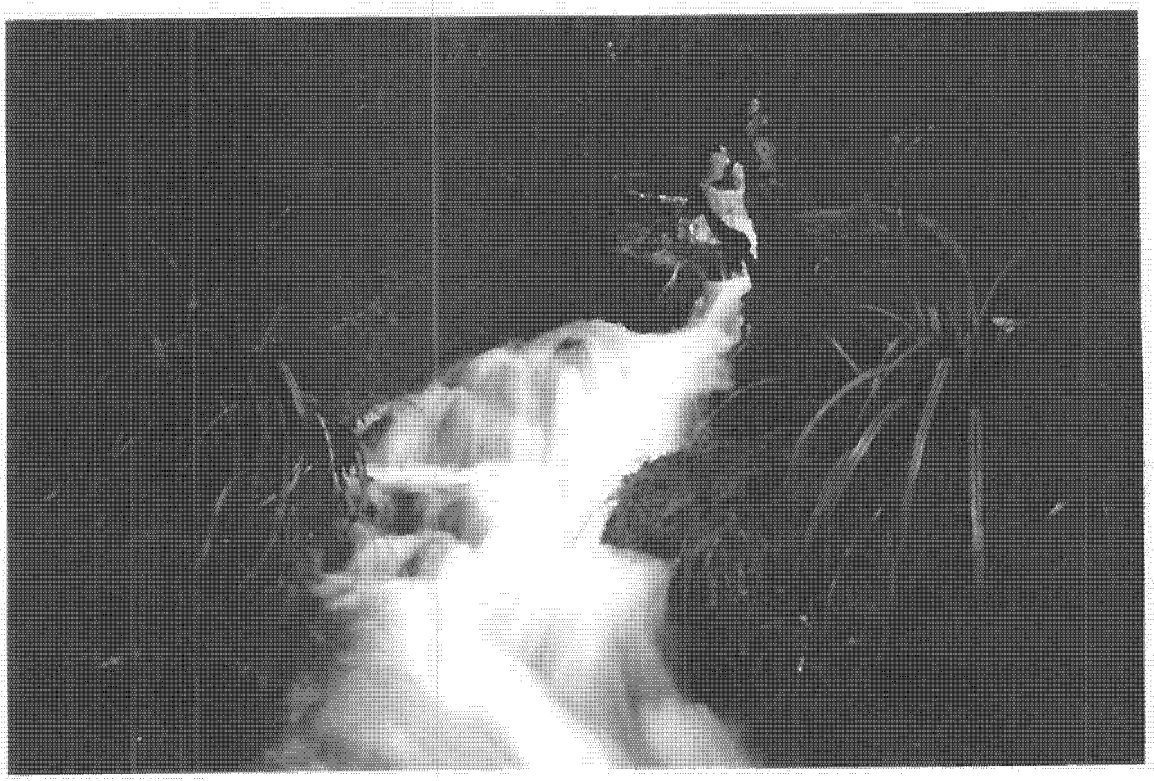


Fig. 4: View of Tim's Creek flowing through mountain beech forest on the slopes of Mt Cassidy. Bryophytes occurred on bedrock in chutes where the stream narrowed considerably. These areas were interspersed with large pools and riffles that displayed great substratum unstability during times of high discharge.

MATERIALS AND METHODS

1. Field Sampling

Five samples were taken from bryophytes and stony riffles at each stream every month for 18 months (July 1986 to December 1987). Bryophytes covering flat rocks were scraped with a razor blade into a 0.01 m^2 Surber sampler (100 µm mesh; Fig. 5a). Stony riffles were sampled to a depth of 10 - 15 cm with a second Surber sampler (area =0.02 m^2, 100 µm mesh) which had a foam flange (3 cm thick) around its base to ensure a firm seal with the substratum (Fig. 5b). Plant material adhering to stones was removed with a nylon brush and added to the collection. The depth of each sample was also measured. From March 1987, water velocity at the upstream right and downstream left-hand sides of each sample area was measured with a current meter (Nixon Instrumentation Limited) 5mm above the substratum.

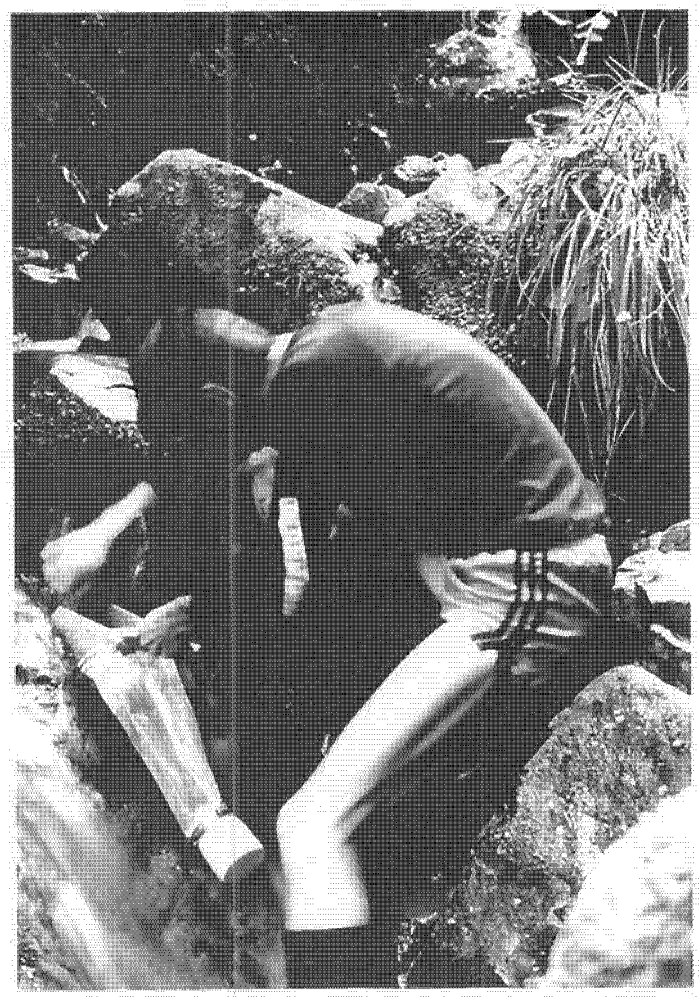
In addition to collecting benthic samples, 2 litre water samples were collected from each stream in acid washed polyethylene containers. Water temperature (maximum, minimum, and monthly spot temperatures) were taken with maximum-minimum thermometers placed in each stream for the duration of the study, and pH was determined in the field (Gallenkamp stick pH meter).

2. Sample Preparation and Analysis

All samples (stream water, bryophytes and riffles) were frozen (-18°C) 3 to 6 hours after collection. Following thawing, stream water was analysed for phenolphthalein alkalinity (Golterman & Clymo 1970), total nitrogen (as nitrate plus nitrite) by reduction through cadmium columns (Smith *et al.* 1982), and dissolved reactive phosphorus (DRP) by the molybdate method with ascorbic acid reduction (Smith *et al.* 1982). The limit of detection for total nitrogen was 1 µg l^{-1} and was 0.4 µg l^{-1} for DRP.

Benthic samples were thawed and organic material in riffle samples was separated from stones and gravel by elutriation, and passed through nested sieves (2.0 mm, 1.0 mm, 500 µm, 250 µm). Material trapped on each sieve corresponded to large, coarse, medium and fine particulate organic matter (LPOM, CPOM, MPOM, FPOM),

Figs 5a,b: Invertebrates associated with bryophytes and riffles were sampled with small surber samplers (100 μm mesh) at each site. Bryophytes were scraped with a razor blade from bedrock areas enclosed by a small (0.01 m^2) sampler (a); riffles were sampled by disturbing inorganic substrata enclosed within a second sampler (0.02 m^2) to a depth of 10-15 cm (b).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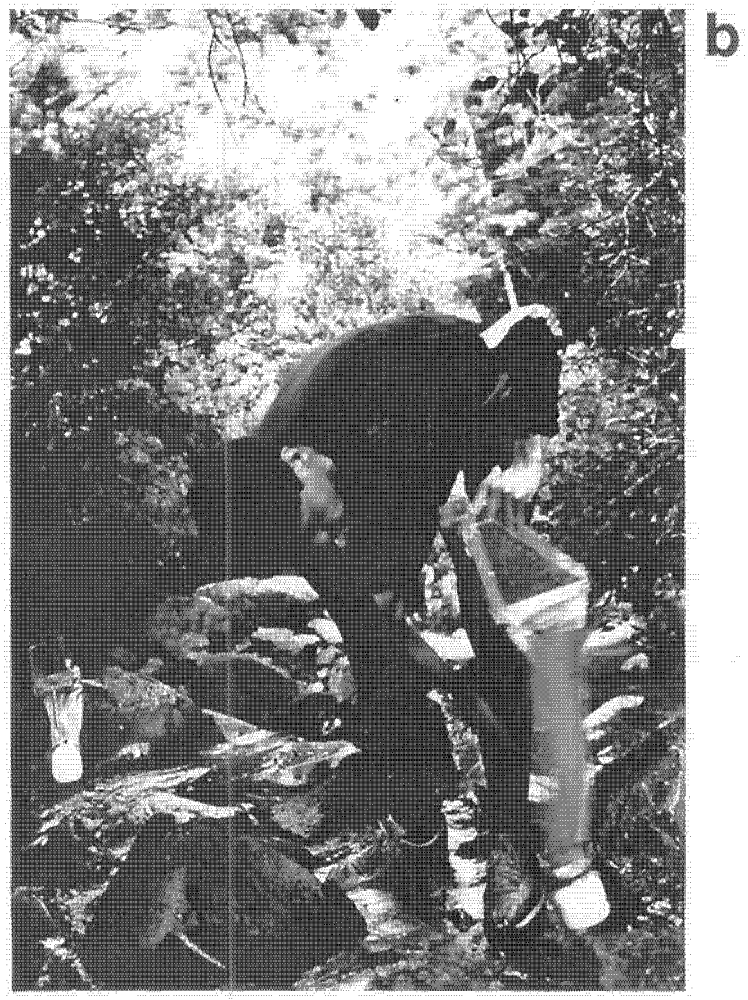
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respectively. Bryophyte samples were teased apart in a metal bowl and vigorously stirred and hosed with high pressure water to dislodge invertebrates, detritus and algae from plant stems before the entire sample including washings was passed through the nested sieves. This process was continued untill no more fine material was dislodged from the bryophytes.

All invertebrates were identified and counted in perspex Bogorov sorting trays (Gannon 1971, Winterbourn & Gregson 1989) under a binocular dissecting microscope (up to 100x magnification). Material collected on the 250 μm mesh sieve was subsampled using a quadripartite splitter and, usually only one subsample was examined. Subsamples that contained large quantities of detritus were split a second time.

Insect taxa were identified to genera and species where possible using the keys of McFarlane (1951), Cowley (1978), Winterbourn & Gregson (1989) and Ordish (1984). However, Ceratopogonidae, Chironomidae, Psychodidae and Stratiomyidae (Diptera) and the Coleoptera Hydrophilidae were not identified below family level. Non-insect taxa were not identified below phylum (Nematoda), class (Ostracoda), or family (Copepoda: Harpacticoida and Rotifera: Bdelloidea), except for Tardigrada which were identified to species using the key of Horning *et al.* (1978).

Dominant bryophytes were identified to genus or species using the keys provided by Inoue & Schuster (1971), Scott & Stone (1976), Engel (1980) and Scott (1985). Small fragments of liverwort belonging to the genera *Lophocolea, Chiloscyphus,* and *Balantiopsis* were also found amongst stems of the dominant bryophytes, but they were not recorded routinely.

Following removal of invertebrates, all remaining material from each sieve was dried at 60°C (48 h), weighed and ashed in a muffle furnace (550°C, 12 h) to determine ash-free dry weight (AFDW). Organic matter data thus represent four size fractions of material trapped in riffles, and total biomass of bryophytes together with associated, accumulated detritus and periphytic algae within their matrices.

3. Statistical Analysis

Data obtained for all environmental parameters (temperature, water velocity, depth, and AFDW of organic matter size fractions), taxonomic richness and invertebrate abundance were normalised by $\log_{10}(x+1)$ transformation prior to statistical analysis. All samples were initially analysed to detect differences in these variables between sites and habitats. Transformed data were analysed by split-plot ANOVA, using time, site and habitat as treatments, reflecting the experimental condition of repeated measures over time from the same habitat within each stream (Sokal & Rohlf 1981).

To determine potential underlying patterns of invertebrate community structure, an ordination analysis was performed using DECORANA (Hill 1979a) on PC-Ord software (McCune 1987). DECORANA arranges all samples in relation to one or more co-ordinate axes, such that their positions along the axes, and relative to each other provide maximum information about their similarity. Because the origin of each sample was known, the influence of site or habitat in producing sample aggregations could be assessed.

Spatial arrangements of samples from bryophytes or riffles, or from Mouse Stream or Tim's Creek were produced such that sample aggregates were associated with high or low scores on the DECORANA axes. Measured environmental variables were then correlated with DECORANA axis sample scores to determine whether specific environmental variables were associated with sample clusters. Abundances of all taxa in each sample were also correlated with DECORANA axis sample scores to determine which species were highly correlated with particular sample groupings, and thus to samples from bryophytes, riffles, Mouse Stream or Tim's Creek.

Samples were also classified by TWINSPAN (Hill 1979b) using the PC-Ord software (McCune 1987). TWINSPAN is a divisive hierarchical method of classification that uses information on all species present in the sample collection (Gauch 1986). Data are first ordinated by reciprocal averaging (RA) and species that characterise the extremes of the RA axis are "chosen". These "indicator species" are then emphasised to polarize the sample collection, which is divided into two aggregates by breaking the ordination

near its middle. The division process is than repeated on the two sample subsets to give four clusters, and so on (Gauch 1986).

The maximum number of indicator species used in my analysis was 7, as too many weaken the polarization whereas too few increase random errors in the data set (McCune 1987). TWINSPAN was terminated after 6 divisions or when each division consisted of five samples.

Because TWINSPAN does not analyse quantitative data directly, the quantitative data were used to create pseudospecies: new variables that represent abundance classes of each species (see e.g., Gauch 1986, McCune 1987, Marchant 1990, Rundle & Hildrew 1990). Following $\log_{10}(x+1)$ transformation of the quantitative data, pseudospecies cut levels were set at 0, 1, 2, 4, and 5 to represent different log abundance classes of each taxon (i.e., to represent densities of 1, 10, 100, 10 000 and 100 000 individuals m^{-2}). Thus a species with a density of 75 individuals m^{-2} would be present at 2 pseudospecies cut levels (0 and 1), whereas densities of 750 individuals m^{-2} would be present at three pseudospecies cut levels (0, 1 and 2). If a certain habitat was always characterised by high densities of a particular species, the pseudospecies representing its density would be chosen as the indicator species.

Analyses were made on pooled seasonal data sets; "winter" (June-August), "spring" (September-November), "summer" (December-February) and "autumn" (March-May). Although the 60 most abundant OTUs were used in all classifications, seasonal variations in the abundances of species resulted in the number of pseudospecies differing seasonally from 132 in winter 1986 to 190 in summer 1986.

RESULTS

Physical factors

Alkalinity in both streams varied over time and was usually higher at Tim's Creek than Mouse Stream (x = 15.64 mg l^{-1} $CaCO_3$ at Tim's Creek; x = 9.54 mg l^{-1} $CaCO_3$ at Mouse Stream; $t=9.92$, $p<0.001$, Fig. 6a).

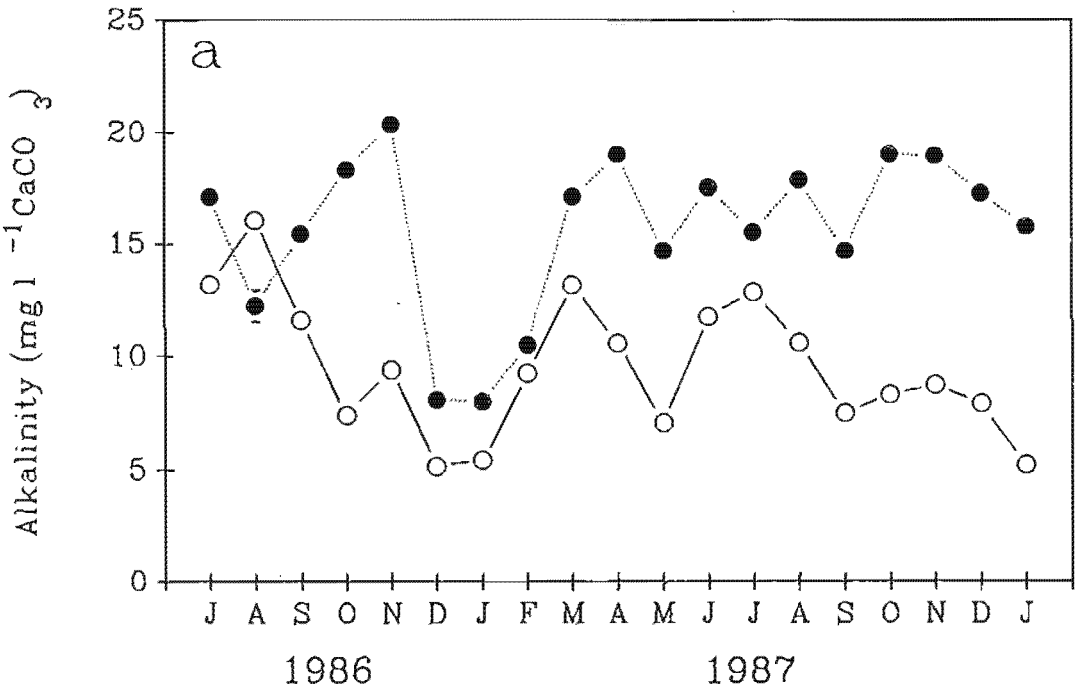


Fig. 6a: Alkalinity of water (as mg l^{-1} $CaCO_3$) collected monthly for 18 months from Mouse Stream (open circles) and Tim's Creek (closed circles); values shown are means of 4 samples, standard errors obscured by symbols.

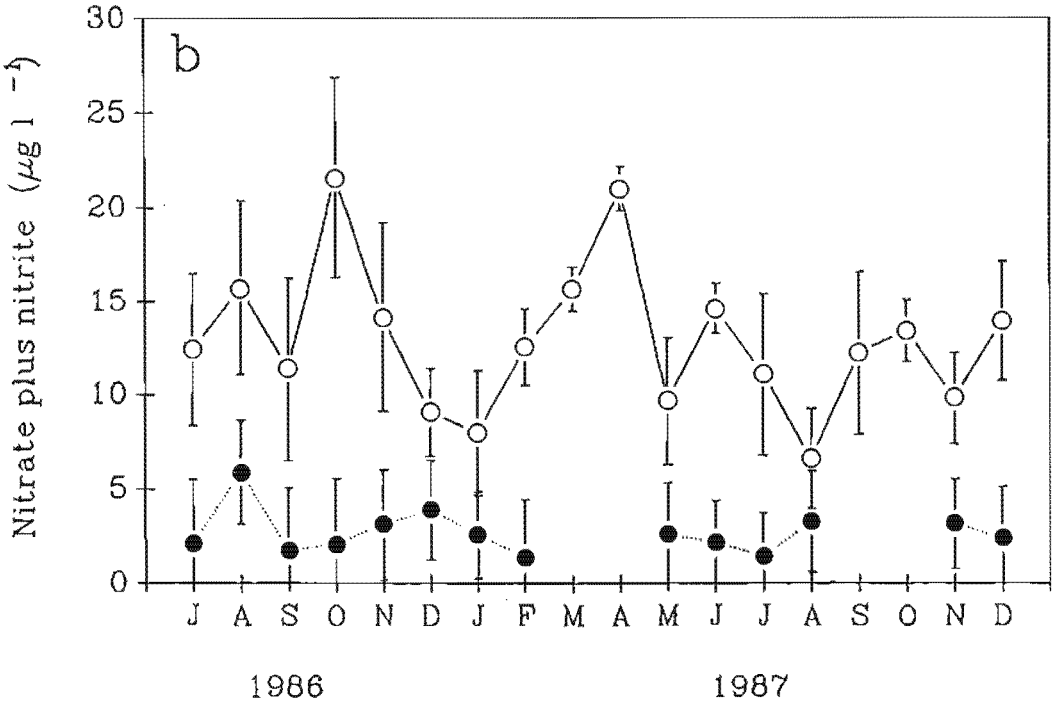


Fig. 6b: Total nitrate/nitrite of water collected monthly for 18 months from Mouse Stream (open circles) and Tim's Creek (closed circles) as determined by reduction through a cadmium column ($x \pm 1SE$, $n = 4$). Values for Tim's Creek were very low and sometimes below the limit of detection (1 µg l^{-1}) as indicated by missing values.

Concentrations of nitrate/nitrate in each stream were always higher at Mouse Stream than Tim's Creek ($x = 12.22\ \mu g\ l^{-1}$ at Mouse Stream, $x = 2.43\ \mu g\ l^{-1}$ at Tim's Creek; $t=11.31$, $p<0.001$). Concentrations fluctuated seasonally, and on four occasions at Tim's Creek, were below the limit of detection (i.e. $<1\ \mu g\ l^{-1}$, Fig. 6b).

Concentrations of dissolved reactive phosphorus were always below the limits of detection ($0.4\ \mu g\ l^{-1}$), although separate analysis by DSIR (Marine and Freshwater, Taupo) indicated that minute quantities of dissolved reactive phosphorus were present in both streams (Table 3).

Water temperature showed clear seasonal patterns at both sites with August minima and January maxima (Fig. 7). Tim's Creek exhibited greater temperature fluctuations than Mouse Stream, (minimum temperature 0.7°C at Mouse Stream , 0.1°C at Tim's Creek; maximum temperature 9.4°C at Mouse Stream, 13.6°C at Tim's Creek), and on one occasion was frozen over in all but very fast flowing areas (Fig. 8) . Average temperatures on days of sampling at Mouse Stream were, however, always colder ($x= 3.7$°C at Mouse Stream ; $x= 5.9$°C at Tim's Creek, $F= 35.7$, $p<0.001$).

Although water depth was related to precipitation on the day of sampling, bryophyte habitats were always shallower than stony riffles. Average depths of bryophyte-covered rocks were 5 cm and 2 cm at Mouse Stream and Tim's Creek, respectively, whereas riffles in both streams were deeper (mean depths, 16 cm at Mouse Stream and 10 cm at Tim's Creek).

Average water velocities were similar in the two streams and were faster above bryophyte covered rocks than in stony riffles ($x= 21$ and $30\ cm\ s^{-1}$ at bryophyte covered sampling sites and 9 and 8 $cm\ s^{-1}$ in riffles at Mouse Stream and Tim's Creek, respectively).

Organic matter

The AFDW of all size fractions of organic matter differed between habitats but not sites. Thus, bryophyte samples contained more total organic matter than riffle samples (mean data for total organic matter; $F= 12.98$, $p<0.001$).

Table 3: Water chemistry* data obtained for the two streams during the study. *Alkalinity values shown are minima and maxima obtained in monthly samples. N & P fractions were analysed by the Taupo DSIR Marine & Freshwater Sciences Laboratory from samples taken at low and high flows on single occasions in 1988.

	MOUSE STREAM		TIM'S CREEK	
	High Flow	Low Flow	High Flow	Low Flow
Dissolved reactive phosphorus ($\mu g\ \ell^{-1}$)	1.9	2.2	1.0	1.6
Dissolved organic phosphorus ($\mu g\ \ell^{-1}$)	0.1	0.9	0.9	0.4
NH_4-N ($\mu g\ \ell^{-1}$)	2.5	0(<0.5)	2.0	2.7
NO_3-N ($\mu g\ \ell^{-1}$)	12.5	16.7	1.4	1.3
Dissolved organic nitrogen ($\mu g/\ell^{-1}$)	49.1	6.8	72.1	11.5
Alkalinity (mg ℓ^{-1} $CaCO_3$)	5.25 (min)	16.0 (max)	8.0 (min)	20.25 (max)

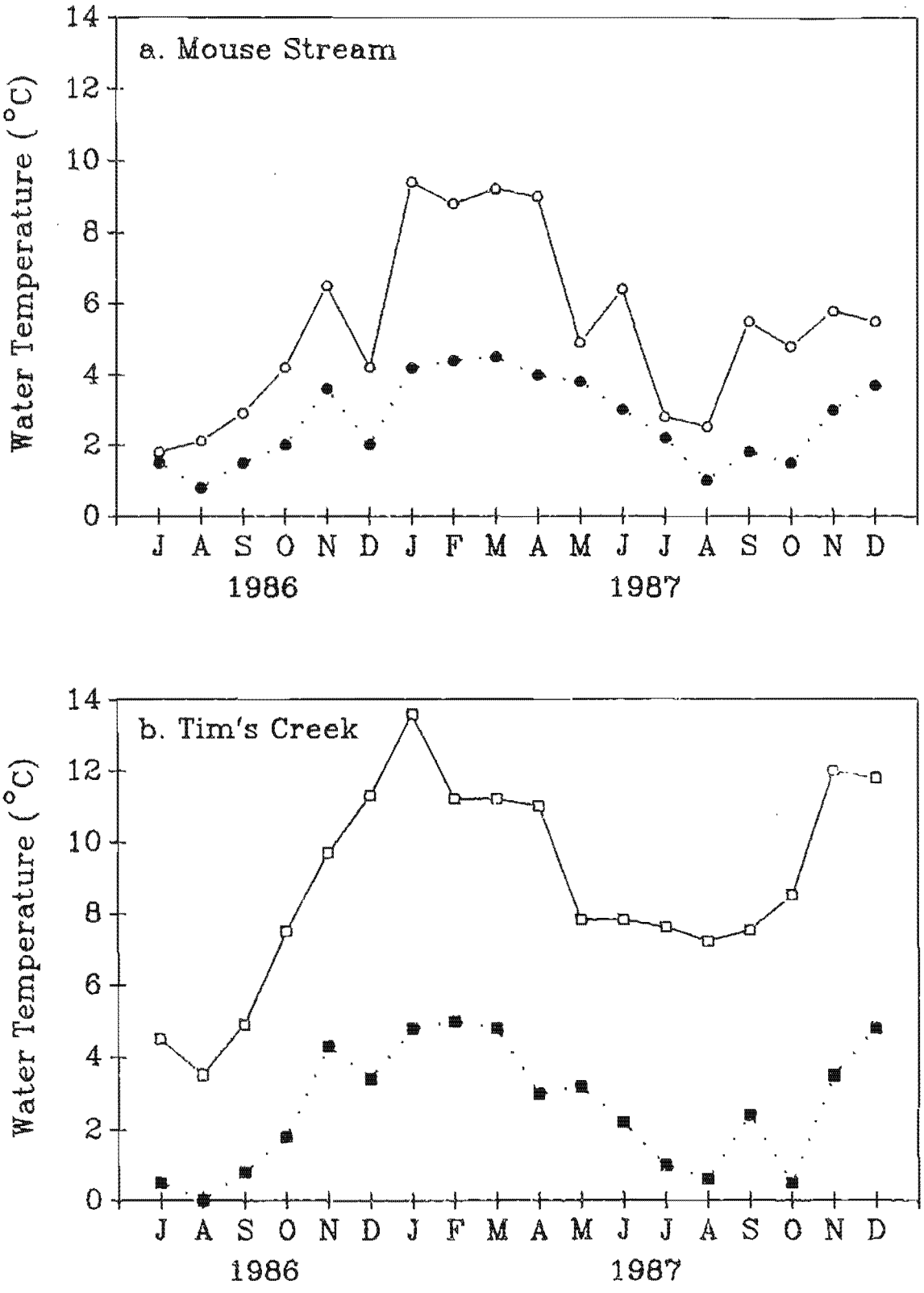
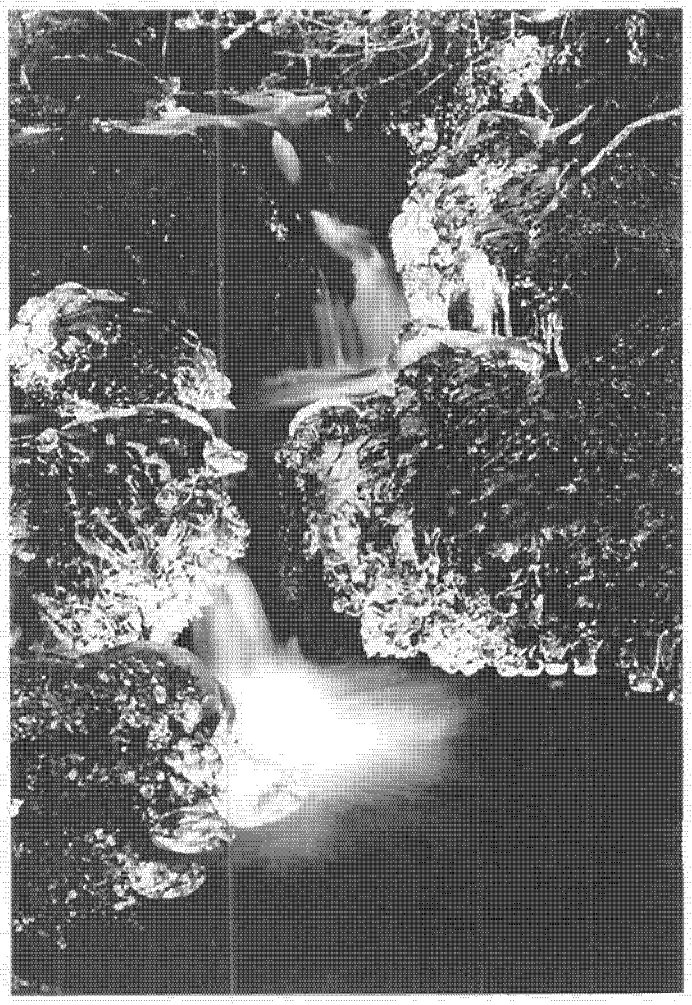


Fig. 7: Monthly maximum and minimum temperatures recorded at a) Mouse Stream, and b) Tim's Creek. Open symbols and solid line = maxima; closed symbols and dotted line = minima.

Figs 8a,b: Air temperatures during winter often drop well below freezing. Tim's Creek occasionally froze over; either in the spray zones around waterfalls (a) or, in extreme cold, the entire stream reach including the large waterfall where it flowed into the Bealey River (b).



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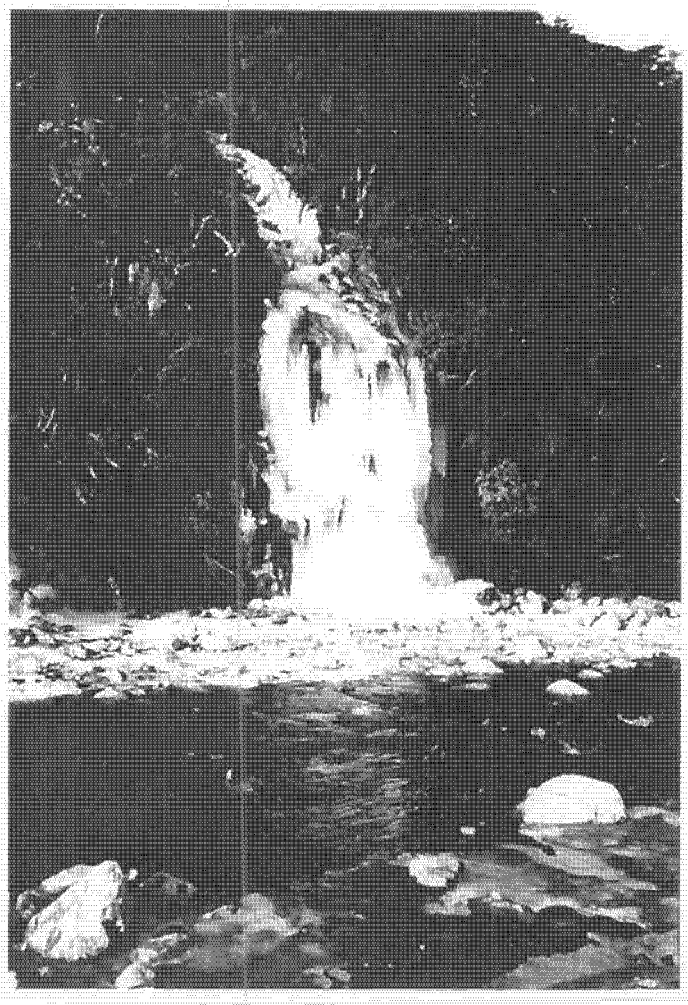

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Organic matter present in bryophyte samples and retained on the 2.0 mm mesh accounted for approximately 75% of total AFDW weight, whereas the smaller fractions representing CPOM, MPOM and FPOM (predominantly detritus) each made up approximately 10% of total organic weight. Clearly most of the organic matter was contributed by the bryophytes themselves. Organic matter collected from stony riffles was also dominated by large particles retained on the 2.0 mm mesh sieve (60% of total weight). CPOM contributed 15% of total weight and smaller size fractions (MPOM and FPOM) each contributed about 10%.

Bryophytes trapped significantly more FPOM than riffles at both sites (x= 20.15 g m^{-2} and 15.46 g m^{-2} in bryophytes; x= 6.61 g m^{-2} and 9.21 g m^{-2} in riffles at Mouse Stream and Tim's Creek, respectively, F= 108.1, $p<0.001$), but quantities of trapped FPOM in both habitats was similar between sites (x= 26.8 g m^{-2} at Mouse Stream; x= 24.7 g m^{-2} at Tim's Creek, F= 0.98, $p>0.05$). Bryophyte samples from Mouse Stream trapped more FPOM than bryophytes from Tim's Creek, but riffle samples from Tim's Creek contained significantly more FPOM than those from Mouse Stream (F= 13.8, $p<0.001$).

AFDW of organic matter fractions from both habitats differed significantly with time (F=1.72, 4.51, 3.22, 1.98, for LPOM, CPOM, MPOM and FPOM, $p<0.01$). However, total organic matter biomass showed no clear seasonal patterns (Figs 7a,b). AFDW of total organic matter in bryophyte samples peaked in December 1986 and August 1987 at Mouse Stream, and in December/January 1986 in Tim's Creek. Total organic matter content of riffles at Mouse Stream was highest in February 1987, and decreased in July of both years. Riffles at Tim's Creek trapped more organic matter in December 1986, and March and April 1987, whereas retention of this material was reduced in late winter and early spring each year.

Temporal fluctuations in the organic matter content of samples from riffles presumably reflect interactions between riparian inputs to each stream and their degree of retention. However, recorded variations in bryophyte standing crop mainly represent sampling variability. They are therefore unlikely to reflect major differences in actual bryophyte standing crops as the plants were always present in both streams and did not show any seasonal dieback.

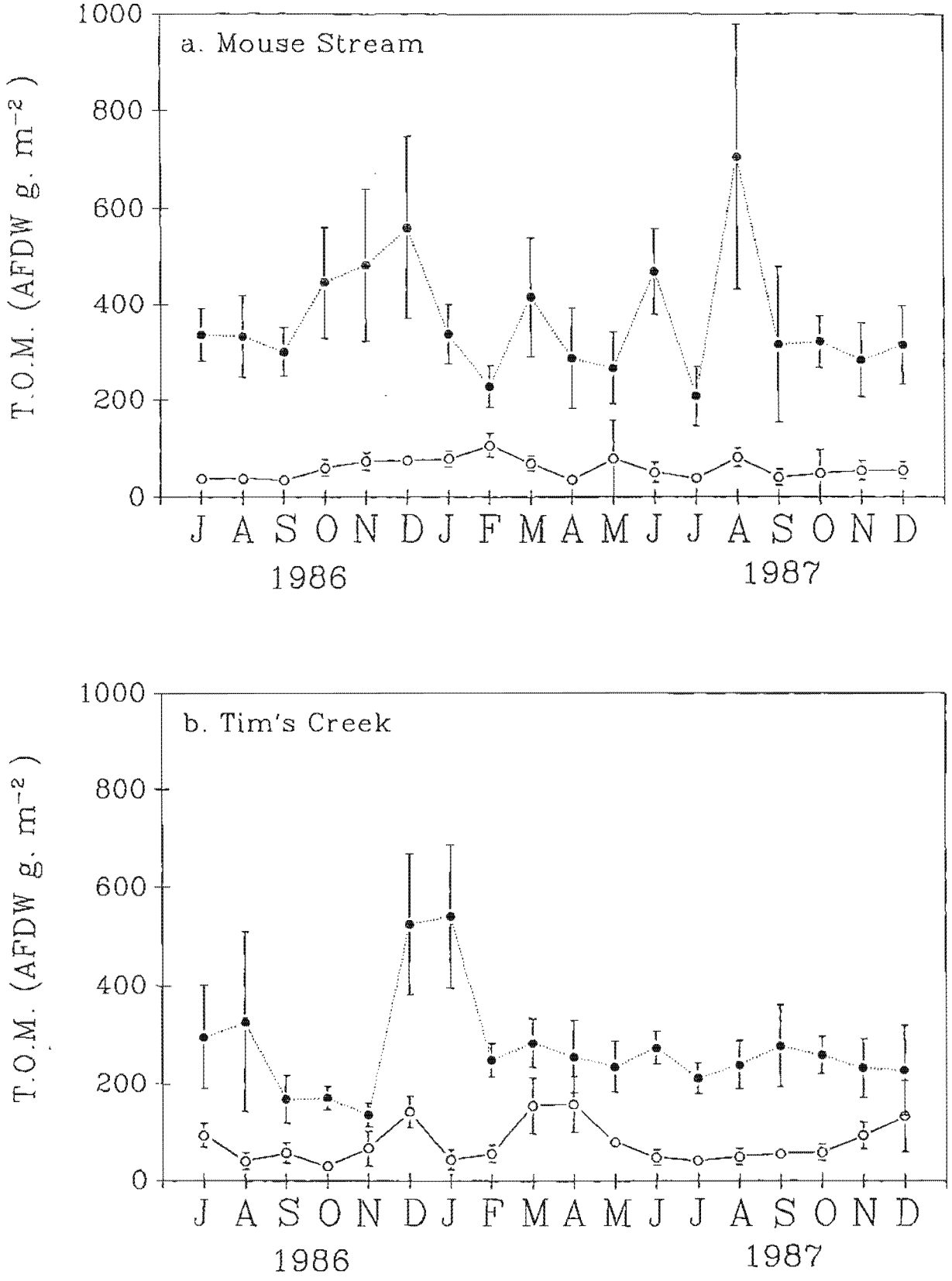


Fig. 9: Ash free dry weight of total organic matter (T.O.M) present in samples collected monthly from bryophyte-covered rocks and bare riffles at a) Mouse Stream and b) Tim's Creek (n = 5, x ± 1SE). Open symbols and solid lines = riffles; closed symbols and dotted lines = bryophytes.

The bryophyte flora

Eleven species of Bryophyta (6 mosses and 5 liverworts) were common in the two streams (Table 4). *C. relaxa* was most common in Mouse Stream and occurred in 81% of samples over the course of the study. *F. rigidulus* and *B. blandum* were the next most common species, and were present in 51% and 25% of samples, respectively. *P. retrospectans* dominated the bryophyte flora of Tim's Creek (73%), and *F. rigidulus* (41%) and *H. paucistipula* (48%) were also common.

At both sites, bryophytes often intermingled and approximately 80% of samples contained more than one taxon. Samples from Mouse Stream contained monospecific growths of *C. relaxa* (15%), *F. rigidulus* (5%) and *B. blandum* (1%), and the liverworts *P. retrospectans* and *H. paucistipula* grew in pure stands in 14% and 5% of samples from Tim's Creek.

The invertebrate fauna

Composition

A total of 94 operational taxonomic units (OTUs) were distinguished from the two streams (Appendix 1). Thirty were Diptera, 26 Trichoptera, 12 Plecoptera and 9 Coleoptera. Larvae of Chironomidae, Tipulidae, Muscidae, Empididae and Simuliidae were the most abundant dipterans, and Hydrobiosidae were the most abundant Trichoptera. Crustaceans (ostracods and copepods) were the dominant non-insect taxa (4 of the remaining 17 OTUs).

Total numbers of taxa collected varied seasonally with no apparent trends, although bryophyte and riffle samples at Mouse Stream followed similar patterns (Figs 10a,b). Most taxa were collected from bryophyte habitats at Tim's Creek (72 OTUs) whereas only 59 were collected from bryophytes at Mouse Stream. Intermediate numbers of OTUs were collected from riffles at both sites (59 at Mouse Stream, 63 at Tim's Creek).

Average taxonomic richness per sample was similar between sites but taxonomic richness differed between sampling trips ($F = 3.20$ $p<0.001$, Fig. 11). Taxonomic richness

Table 4: Frequency of occurence (%) of bryophyte taxa* collected in 5 replicate Surber samples taken monthly for 18 months from each site from July 1986 until December 1987.

BRYOPHYTE TAXA	MOUSE STREAM	TIM'S CREEK
CLASS: ANTHOCEROTAE (Hornworts)		
ORDER: Anthocerotales		
FAM: Anthocerotaceae		
Anthoceros laevis L.	-	21
CLASS: HEPATICAE (Liverworts)		
SUBCLASS: Jungermanniae		
ORDER: Jungermanniales		
FAM: Geocalycaceae		
Lophocolea planiscula (Hook. f. & Taylor) Taylor et Gottsche et al.	8	20
Chiloscyphus sp.	-	10
Hepatostolonophora paucistipula (Rodway)	-	47
FAM: Plagiochilaceae		
Plagiochila retrospectans Nees	-	73
P. circinalis (Lehm.) Lehm & Lindenb	-	8
CLASS: MUSCl (Mosses)		
SUBCLASS: Bryidae		
ORDER: Hypnobryales		
FAM: Amblystegiaceae		
Cratoneuropsis relaxa (Hook.f.Wils.) Fleisch in Broth	81	-
ORDER: Fissidentales		
FAM: Fissidentaceae		
Fissidens rigidulus Hook.f.& Wils.	51	-
ORDER: Eubryales		
FAM: Bryaceae		
Bryum blandum Hook.f.& Wils.	25	-
ORDER: Hookeriales		
FAM: Hookeriaceae		
Pterygophyllum dentatum (Hook.f. & Wils.) Dix	-	11
Distichophyllum pulchellum (Hampe) Mitt	-	6

*Only those taxa making up >5% of each sample were recorded. Two or more taxa often occurred together in the same sample, thus the percentage occurrence values exceed 100%.

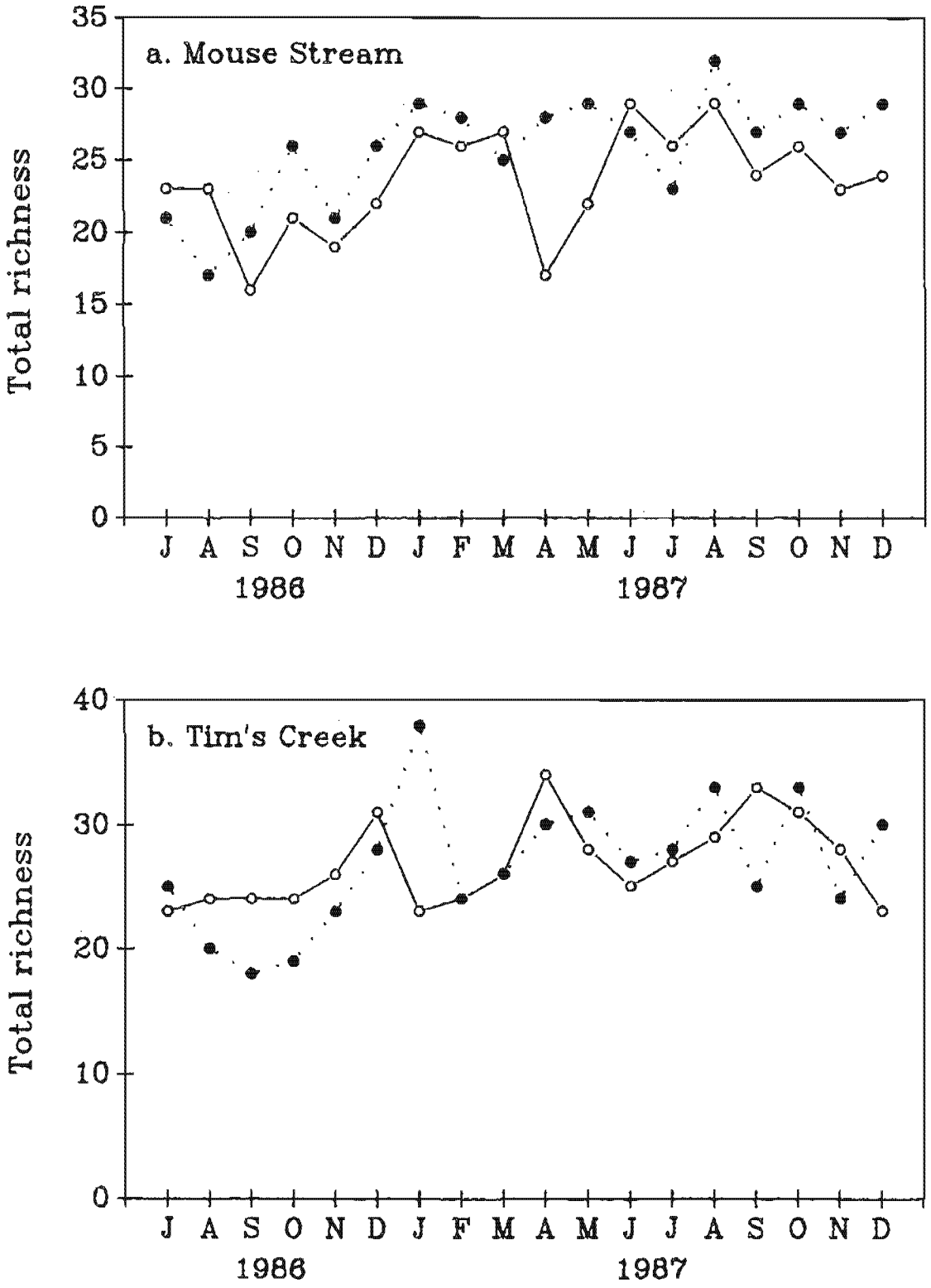


Fig. 10: Total numbers of operational taxonomic units (OTUs) collected monthly from bryophyte and riffle areas at, a) Mouse Stream and b) Tim's Creek. Symbol conventions as in Fig. 9.

differed only between bryophyte and riffle habitats at Mouse Stream ($F= 7.17$, $p<0.001$), where bryophytes ($x= 15.4$ OTUs) supported more taxa than riffles ($x= 12.8$ OTUs).

Relative abundance

Of the invertebrate OTUs collected, the Chironomidae was the most abundant taxon at both sites (56.8% of total invertebrate density), followed by Nematoda (19.0%), Copepoda (7.4%), Ostracoda (3.7%), and Hydracarina (2.4%). A stonefly, *Zelandobius* sp. was the sixth most abundant taxon collected (1.8%).

Bryophyte samples taken from both streams were dominated by larval Chironomidae (57.6% at Mouse Stream, 63% at Tim's Creek). Non-insects were next most abundant at Mouse Stream (Nematoda 22.1%, Copepoda 9%, Ostracoda 2.8%, Tardigrada 2.4%), whereas Nematodes (12.5%), Hydracarina (5.9%), larval Empididae sp.B (3.8%) and pupating chironomids (2.7%) were common at Tim's Creek (Table 5).

Similarly, stony riffle faunas at both sites were dominated by chironomids (40.9% at Mouse Stream, 31% at Tim's Creek). Other insect larvae were relatively more abundant in riffles than bryophyte samples (e.g. *Deleatidium*, *Nesameletus*, and *Zelandobius* spp. (11.3%, 4.8%, 7.3% respectively at Mouse Stream; 8.3%, 3.4%, 3.9% respectively at Tim's Creek; Table 5).

Invertebrate densities

Total invertebrate densities in the two streams changed monthly, although no consistent trends were evident. Densities were always higher in Mouse Stream than Tim's Creek and in both streams more invertebrates inhabited bryophyte-covered rocks (per unit area) than stony riffles (Figs 12a,b). At Mouse Stream, invertebrate densities peaked twice during the study (February and August 1987, Fig. 12a) primarily as a result of increases in chironomid abundance (Fig. 13a). Fluctuations in total invertebrate density at Tim's Creek were not as great, although increases in density were observed twice (January and November 1987; Fig 12b) when chironomid abundance was maximal (Fig. 13b). Densities of pupating chironomids increased substantially in

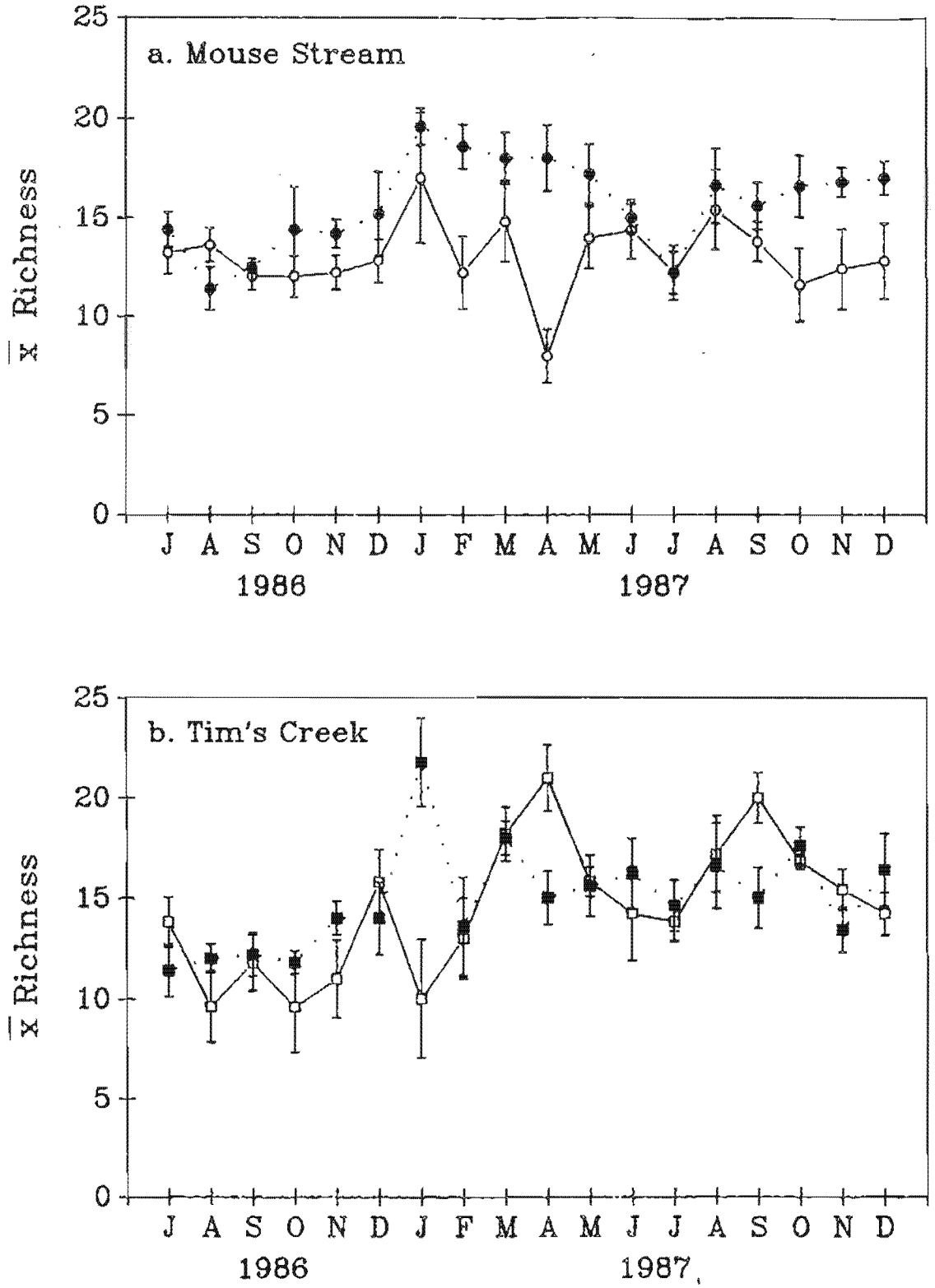


Fig. 11: Average taxonomic richness per sample collected monthly from bryophyte and riffle areas at a) Mouse Stream and b) Tim's Creek; ($\bar{x} \pm 1SE$, n = 5). Symbol conventions as in Fig. 9.

Table 5: Percentage contribution of the 10 most common invertebrate taxa taken from bryophyte and riffle habitats at each site from July 1986 to December 1987. (n = 5 Surber Samples per site and habitat per month.

	HABITAT			
SITE	BROYPHYTES	%	RIFFLES	%
MOUSE STREAM	Chironomidae (larvae)	57.6	Chironomidae (larvae)	40.9
	Nematoda	12.1	Ostracoda	17.3
	Copepoda	9.0	*Deleatidium* sp.	11.3
	Ostracoda	2.8	*Zelandobius* sp.	7.3
	Tardigrada	2.4	Nematoda	6.3
	Zelandobius sp.	1.4	Copepoda	4.9
	Hydracarina	1.1	*Nesameletus* sp.	4.8
	Empididae sp. B	0.9	Hydracarina	3.3
	Zelandoperla spp.	0.7	Hydrobiosidae	0.9
	Chironomidae (pupae)	0.3	Chironomidae (pupae)	0.6
	Average abundance (m^{-2})	218 400	Average abundance (m^{-2})	20 870
TIM'S CREEK	Chironomidae (larvae)	63	Chironomidae (larvae)	31
	Nematoda	12.5	Hydracarina	11.4
	Hydracarina	5.9	Ostracoda	8.8
	Empididae sp. B	3.8	*Deleatidium* sp.	8.3
	Chironomidae (pupae)	2.7	Copepoda	6.6
	Copepoda	1.5	Nematoda	6.1
	Zelandoperla sp.	1.4	*Zelandobius* sp.	3.9
	Austrosimulium ungulatum	1.2	*Cristaperla fimbria*	3.7
	Zelandobius sp.	1.1	*Nesameletus* sp.	3.4
	Ostracoda	0.7	Helodidae sp. C.	3.1
	Average abundance (m^{-2})	53 450	Average abundance (m^{-2})	7 360

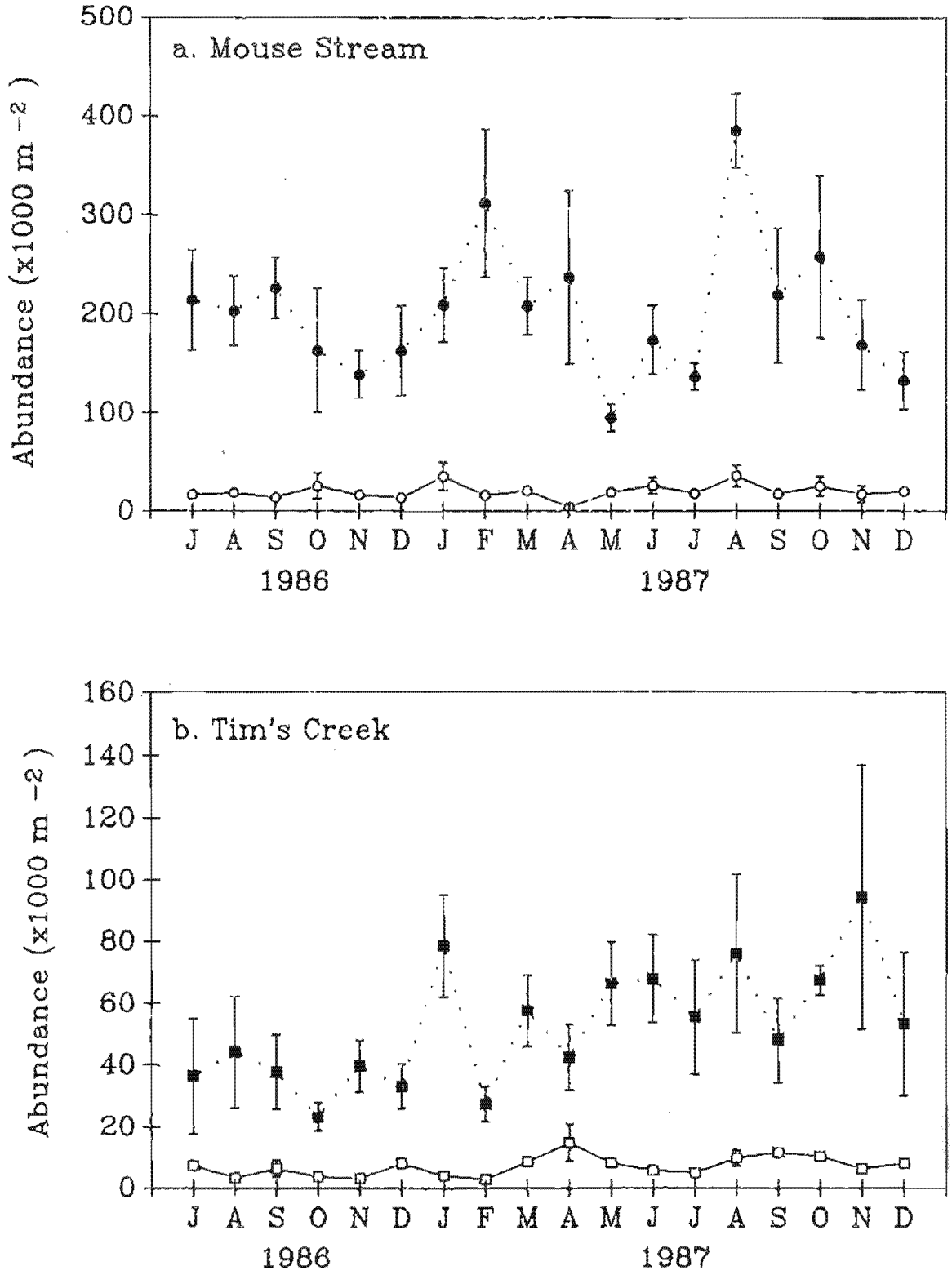


Fig. 12: Total invertebrate densities each month in bryophyte and riffle samples from a) Mouse Stream and b) Tim's Creek; ($\bar{x} \pm$ 1SE, n = 5). Symbol conventions as in Fig. 9.

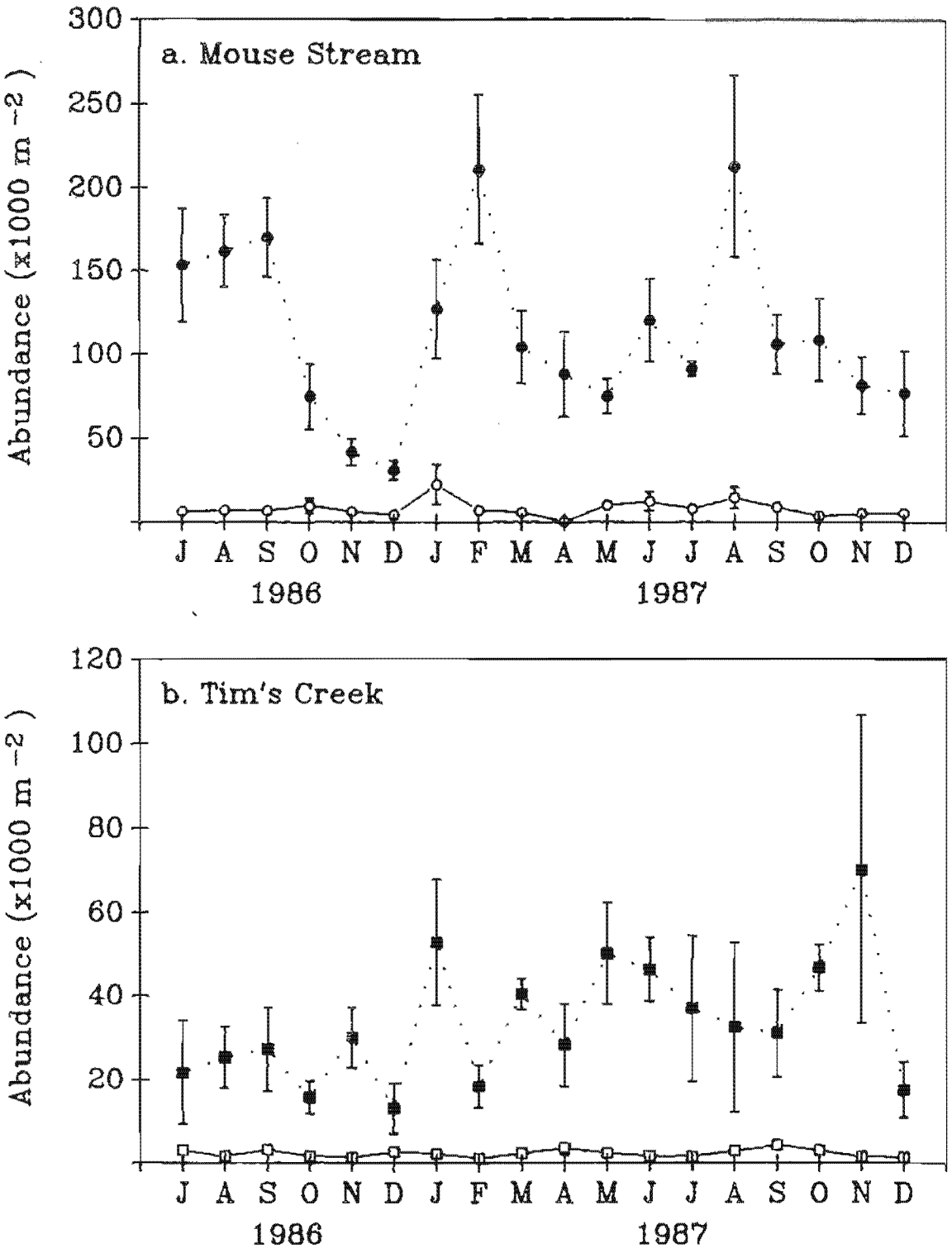


Fig. 13: Densities of Chironomidae larvae each month in bryophyte and riffle samples from a) Mouse Stream and b) Tim's Creek; ($x \pm 1SE$, $n = 5$). Symbol conventions as in Fig. 9.

November-December (1986) and August-September (1987) at both streams (Figs 14a,b), and were followed by peaks in larval density about 2 months later.

Invertebrate densities, excluding chironomids, displayed distinct winter minima at Mouse Stream (Fig. 15a), a pattern also displayed by nematodes, copepods and tardigrades, the next most dominant OTUs (Figs 16-18). However, no comparable temporal changes in density were evident at Tim's Creek (Figs 15-17), perhaps as a consequence of life history phenomena.

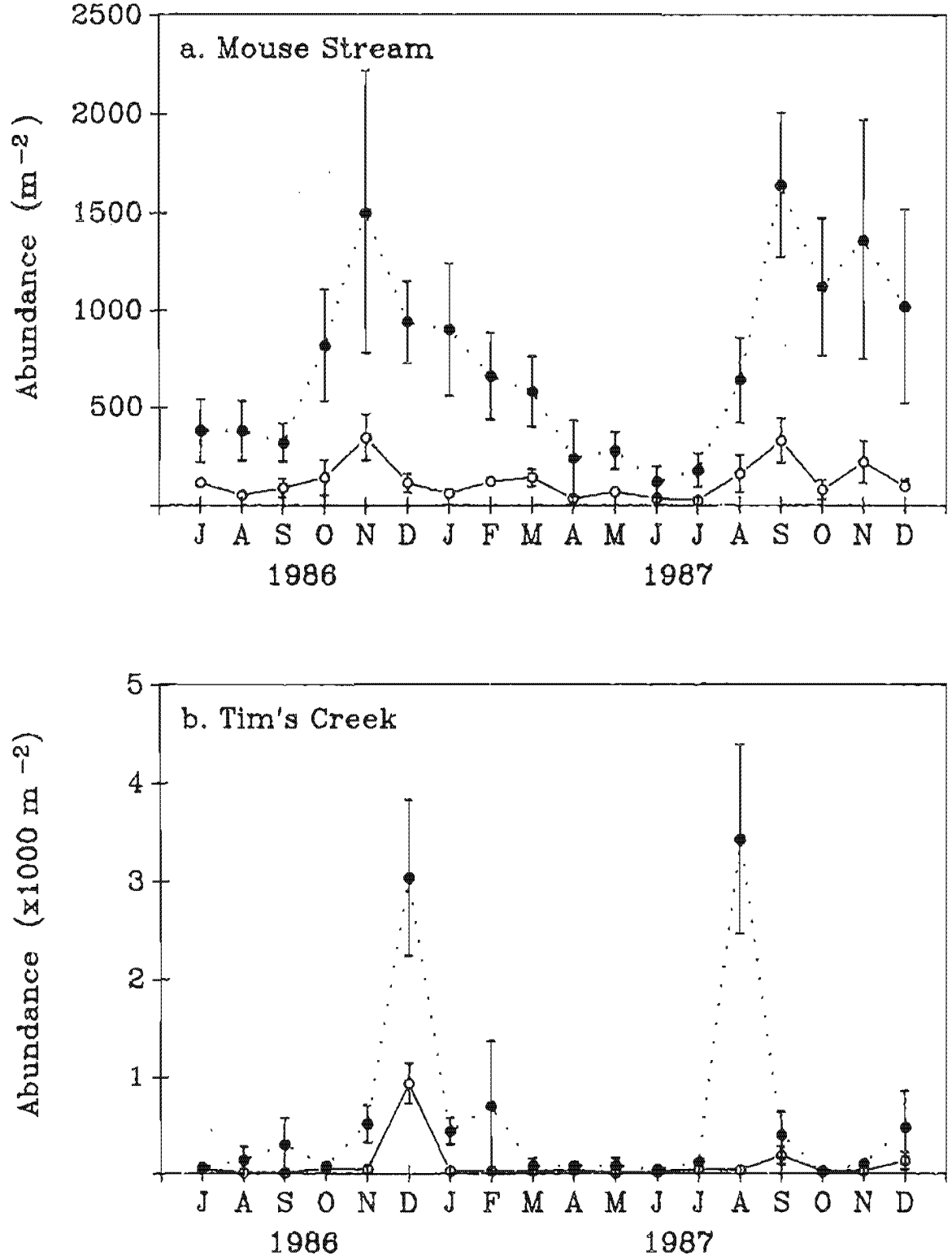


Fig. 14: Densities of Chironomidae pupae each month in bryophyte and riffle samples from a) Mouse Stream and b) Tim's Creek; ($x \pm 1SE$, $n = 5$). Symbol conventions as in Fig.9.

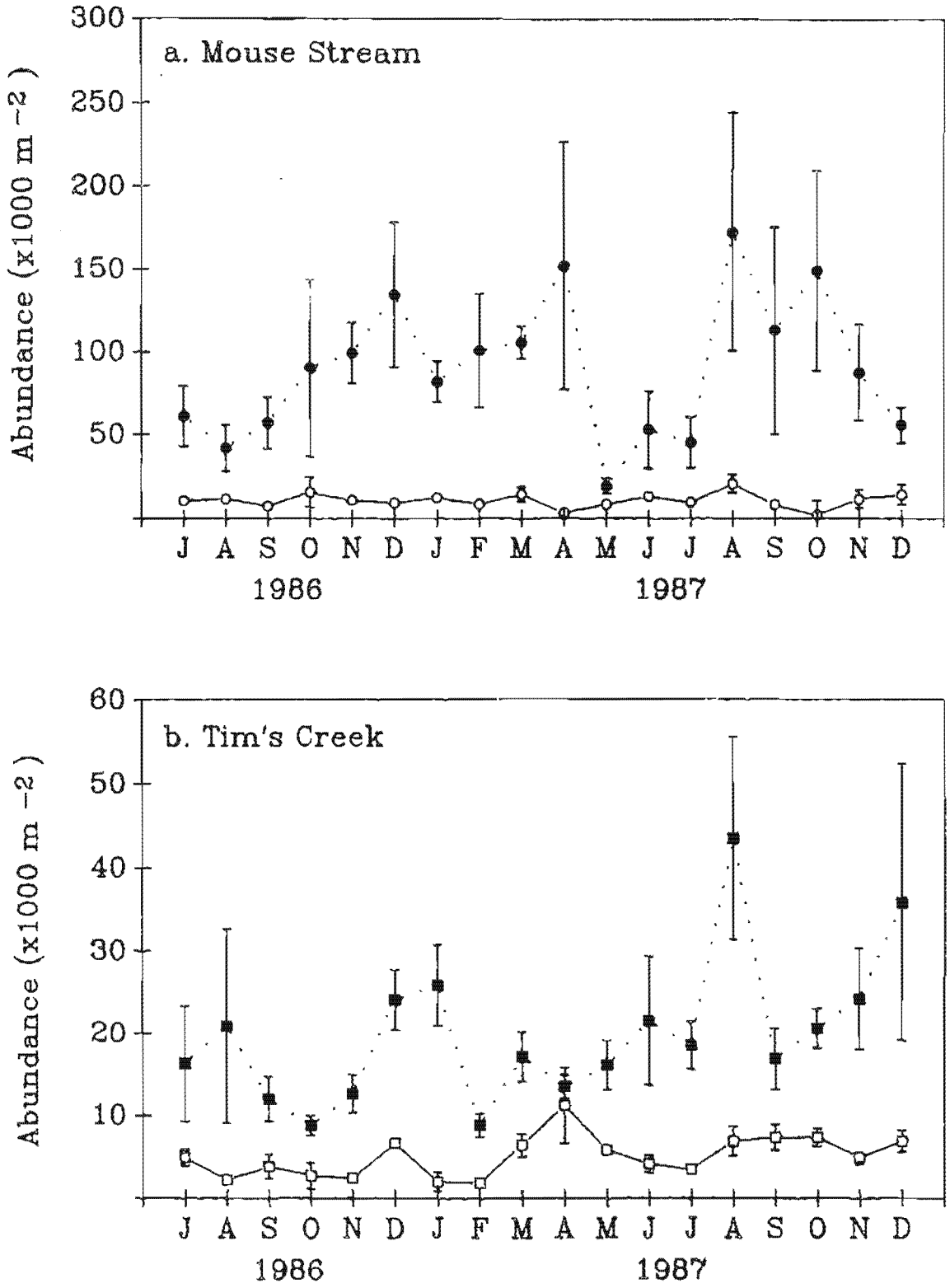


Fig. 15: Total invertebrate densities excluding Chironomidae each month in bryophyte and riffle samples from a) Mouse Stream and b) Tim's Creek; ($x \pm 1SE$, $n = 5$). Symbol conventions as in Fig. 9.

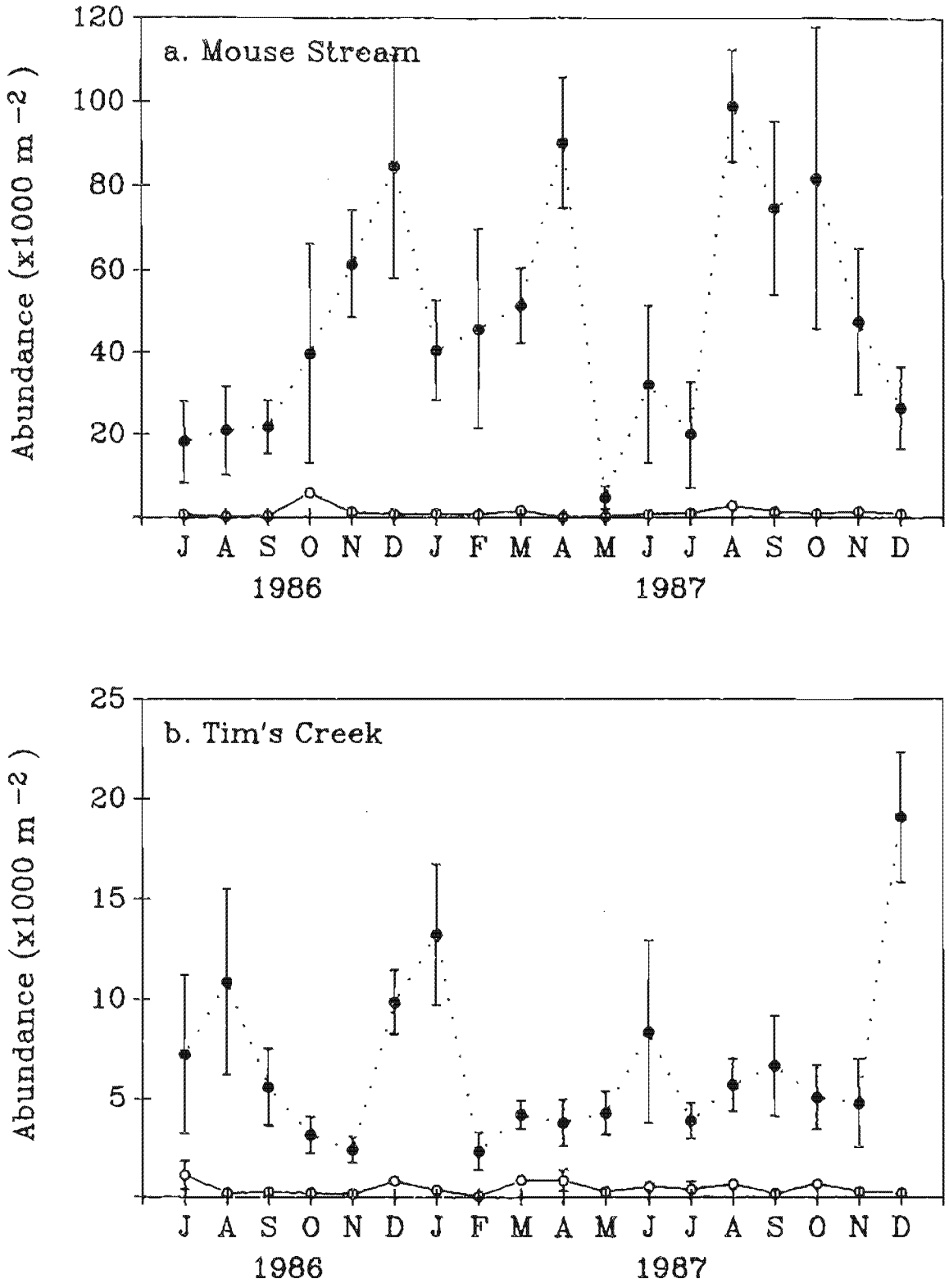


Fig. 16: Densities of Nematoda each month in bryophyte and riffle samples from a) Mouse Stream and b) Tim's Creek; ($\bar{x} \pm 1SE$, n = 5). Symbol conventions as in Fig. 9.

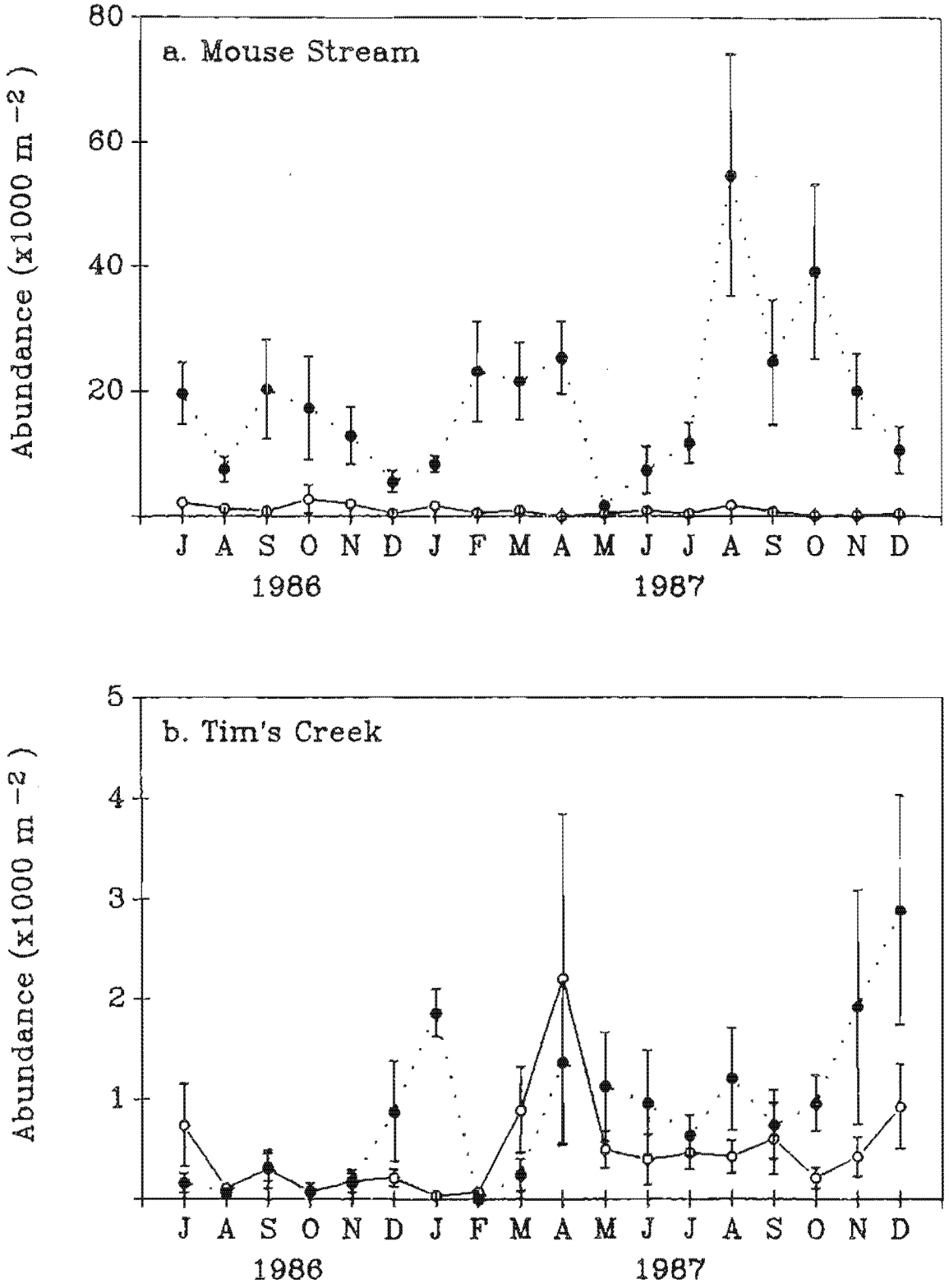


Fig. 17: Densities of copepoda each month in bryophyte and riffle samples from a) Mouse Stream and b) Tim's Creek; ($x \pm 1SE$, $n = 5$). Symbol conventions as in Fig. 9.

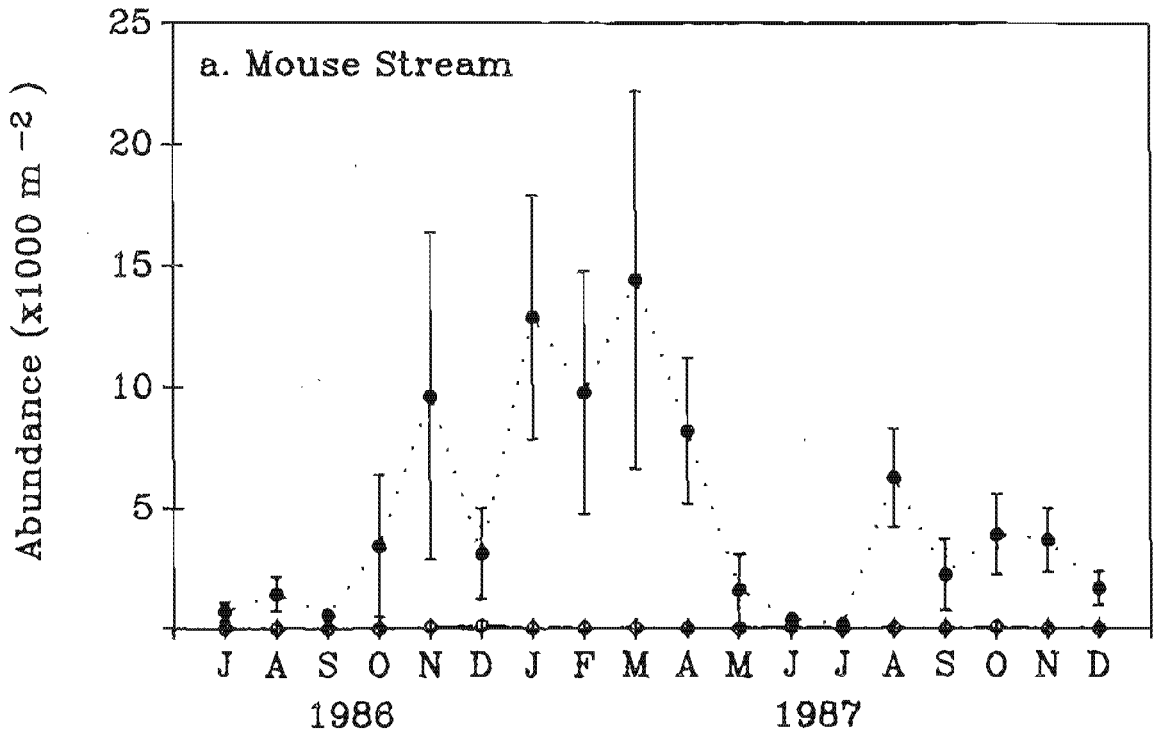


Fig. 18: Densities of Tardigrada each month in bryophyte and riffle samples from Mouse Stream; ($x \pm 1SE$, $n = 5$). Symbol conventions as in Fig. 9.

Community Ordination

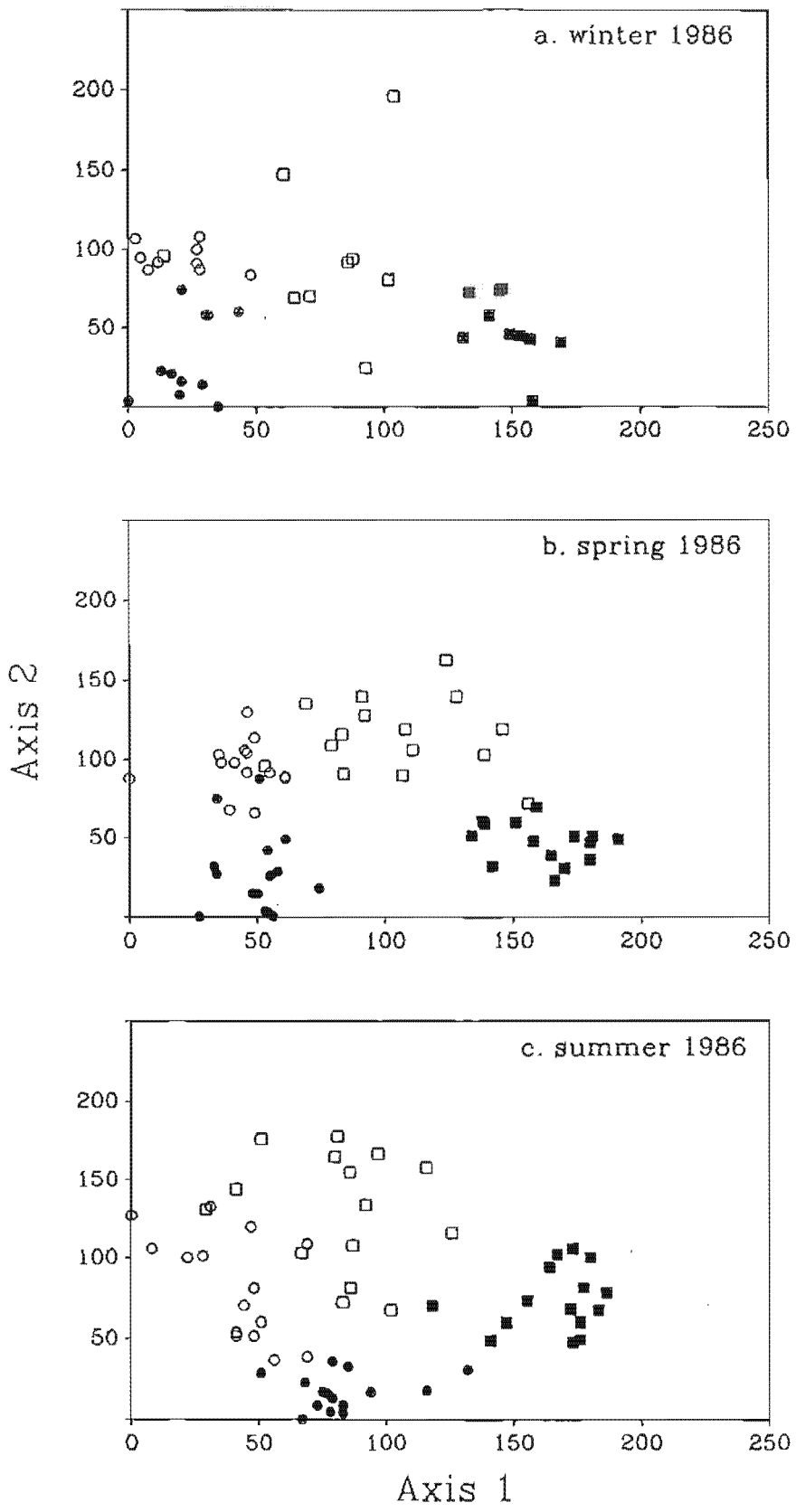
Sample aggregation

Data were ordinated firstly to establish whether samples from similar locations would aggregate into discrete groups, and secondly to identify environmental factors associated with the aggregations. Samples from each season aggregated on DECORANA axes 1 and 2 primarily on the basis of site or habitat similarity (Figs 19 a-f). Segregation was most apparent on axes 1 and 2 which explained 54.6% and 30.8%, respectively of the variation in sample spread on each axis for the average of all seasons analysed (Table 6).

Sample aggregations in winter and spring 1986 were determined primarily by site differences on axis 1, and displayed significant correlations to temperature here (Table 7). Sample spread on axis 2 were delineated by habitat differences (Figs 19 a,b).

Conversely, sample aggregations from winter and spring 1987 were delineated by habitat differences on axis 1 and site differences on axis 2 (Figs 19 e,f). In both seasons, bryophyte samples all had low axis 1 scores, and were correlated with higher organic matter content and shallow, fast water (Table 7). Samples aggregated by site on axis 2 with significant correlations to warmer water temperature and greater organic matter content (Table 7).

Although summer 1986 and autumn 1987 samples formed discrete clusters (Fig 17 c,d), these clusters were not clearly associated with specific sites or habitats. However, bryophyte samples taken from Tim's Creek clustered together on axis 1 with high and low scores. These clusters represented samples taken from warm waters with a high organic matter biomass, as reflected by the significant correlations to water temperature and organic matter fractions (Table 7). Sample clustering on axis 2 reflected habitat differences in summer and a combination of site and habitat differences in autumn, with positive correlations to water depth (both seasons) and water temperature reflecting deeper water in riffles and warmer temperatures at Tim's Creek (Table 7).



Figs 19a-f: DECORANA ordination of samples collected monthly from bryophytes (shaded symbols) and riffles (open symbols) in Mouse Stream (circles) and Tim's Creek (squares) showing sample clustering along axes 1 and 2. Six DECORANA analyses were conducted to examine seasonality of the distributions: a) = winter 1986, b) = spring 1986, c) = summer 1986, d) = autumn 1987, e) = winter 1987, f) = spring 1987.

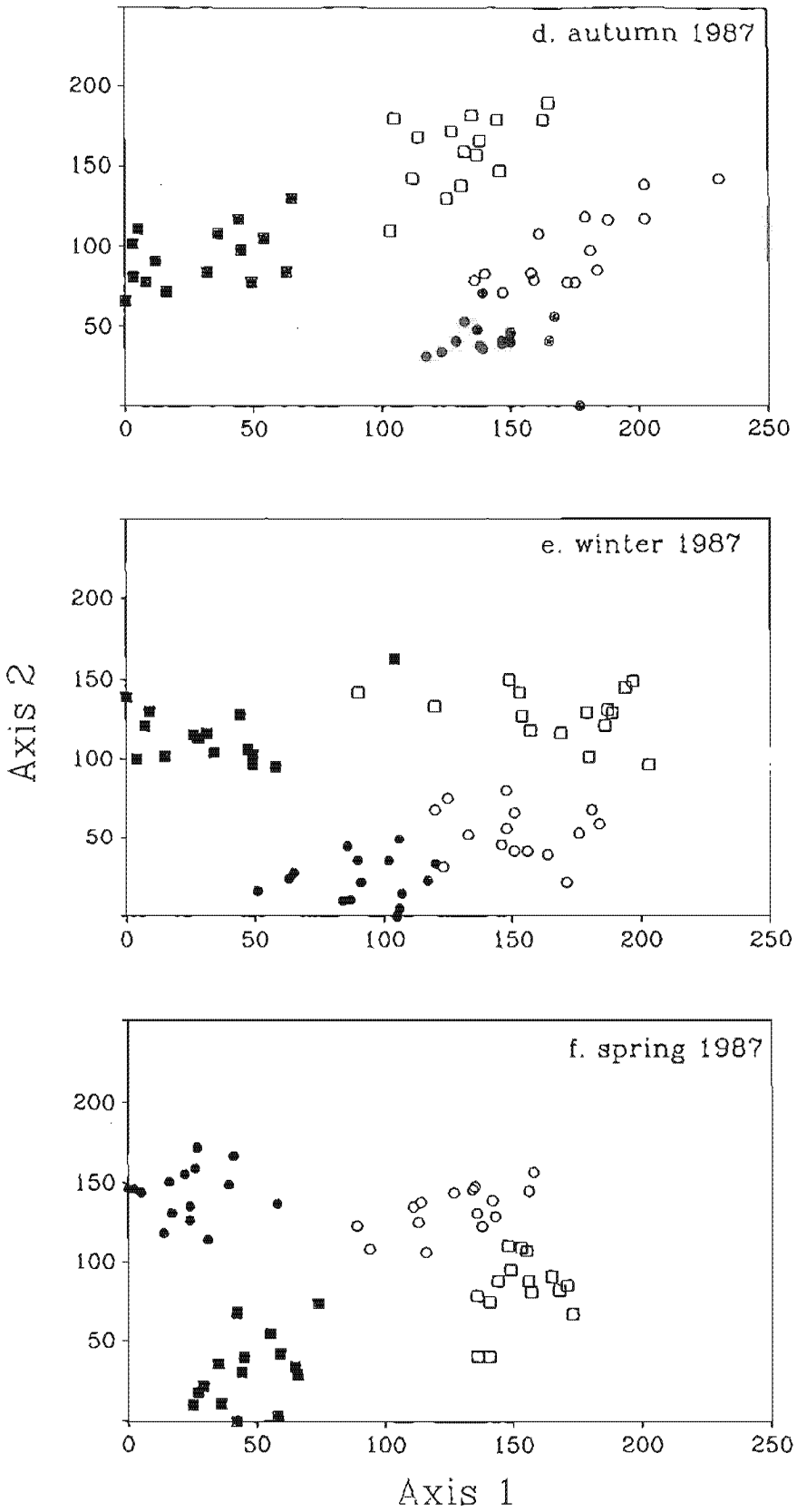

d. autumn 1987
e. winter 1987
f. spring 1987
Axis 2
Axis 1
0
50
100
150
200
250

Table 6: Percentage variation in the 6 seasonal data sets explained by the first 3 DECORANA axes.

Season	Axis 1	Axis 2	Axis 3
Winter 1986	59.1	23.6	17.3
Spring 1986	45.4	37.0	17.6
Summer 1986	60.6	25.5	13.9
Autumn 1987	48.8	37.2	13.9
Winter 1987	59.1	28.6	12.3
Spring 1987	54.7	32.8	12.4
mean % variation	54.6	30.8	14.6
cumulative % variation	54.6	85.4	100.0

Table 7: Significant ($p<0.05$) Pearson correlation coefficients (r) between DECORANA axes 1 and 2 and selected environmental variables taken from each habitat during the study. At the top of each column is a description of the sample clusters on each axis, showing aggregations with low axis scores (-) or high axis scores (+); MS = Mouse Stream, TC = Tim's Creek, B = bryophytes, R = riffles. Values for current velocity were not measured until autumn 1987 (NM).

	Winter 1986			Spring 1986				Summer 1986				Autumn 1987				Winter 1987				Spring 1987			
	Axis 1		Axis 2	Axis 1		Axis 2		Axis 1		Axis 2		Axis 1		Axis 2		Axis 1		Axis 2		Axis 1		Axis 2	
	MS	TC		MS	TC	B	R	rest	TCB	B	R	TCB	rest	MSB	TCR	B	R	MS	TC	B	R	TC	MS
	-	+		-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	+
LPOM									.518			-.300				-.346				-.625		.296	
CPOM									.416							-.375				-.422		.307	
MPOM									.445							-.285		-.278		-.575		.287	
FPOM									.402									-.283		-.312		.282	
max. temp.		.812			.639				.528			-.320		.319					.733			-.697	
min. temp.	-.652								.297				-.292				-.434						
present temp.		.483	.385		.422				.414			-.535		.416					.572			-.676	
water depth	-.321			-.265		.426		-.578		.316		.479		.359		.654				.611		.336	
current velocity	NM		NM	NM		NM		NM		NM		-.672		-.329		-.738				-.603		-.365	

OTU composition: site and habitat differences

Correlations between OTUs and each DECORANA axis were made to assess which taxa were strongly correlated with sample aggregations. Because each axis corresponded with specific sites or habitats, it was possible to determine which taxa were most frequently associated with bryophytes and riffles at each site (Table 8). Abundances of 34 taxa were significantly correlated with samples from Tim's Creek, whereas only 20 taxa were correlated with samples from Mouse Stream. More taxa were correlated with samples from bryophytes (27) than riffles (20). Most taxa were significantly correlated with site or habitat aggregations in less than half the seasons analysed, but some taxa exhibited such correlations in most, or all seasons (Table 8), indicating a high preference for these areas.

Community Classification

TWINSPAN dendrograms

The principal objective of this study was to investigate whether discrete invertebrate communities existed in bryophyte and riffle habitats at each site. Consequently, sample divisions based on differences related to sample site and habitat location are considered, whereas divisions of TWINSPAN groups based solely on seasonal differences between samples are not considered below. Groups made up of samples from one location, irrespective of collection season were regarded as being TWINSPAN "end groups".

At each TWINSPAN level, the percentage of samples classified to these "end groups" was calculated. From data for all six seasons, only 4% of samples were classified to end groups after level 1, but 89% were classified after level 4 (Table 9).

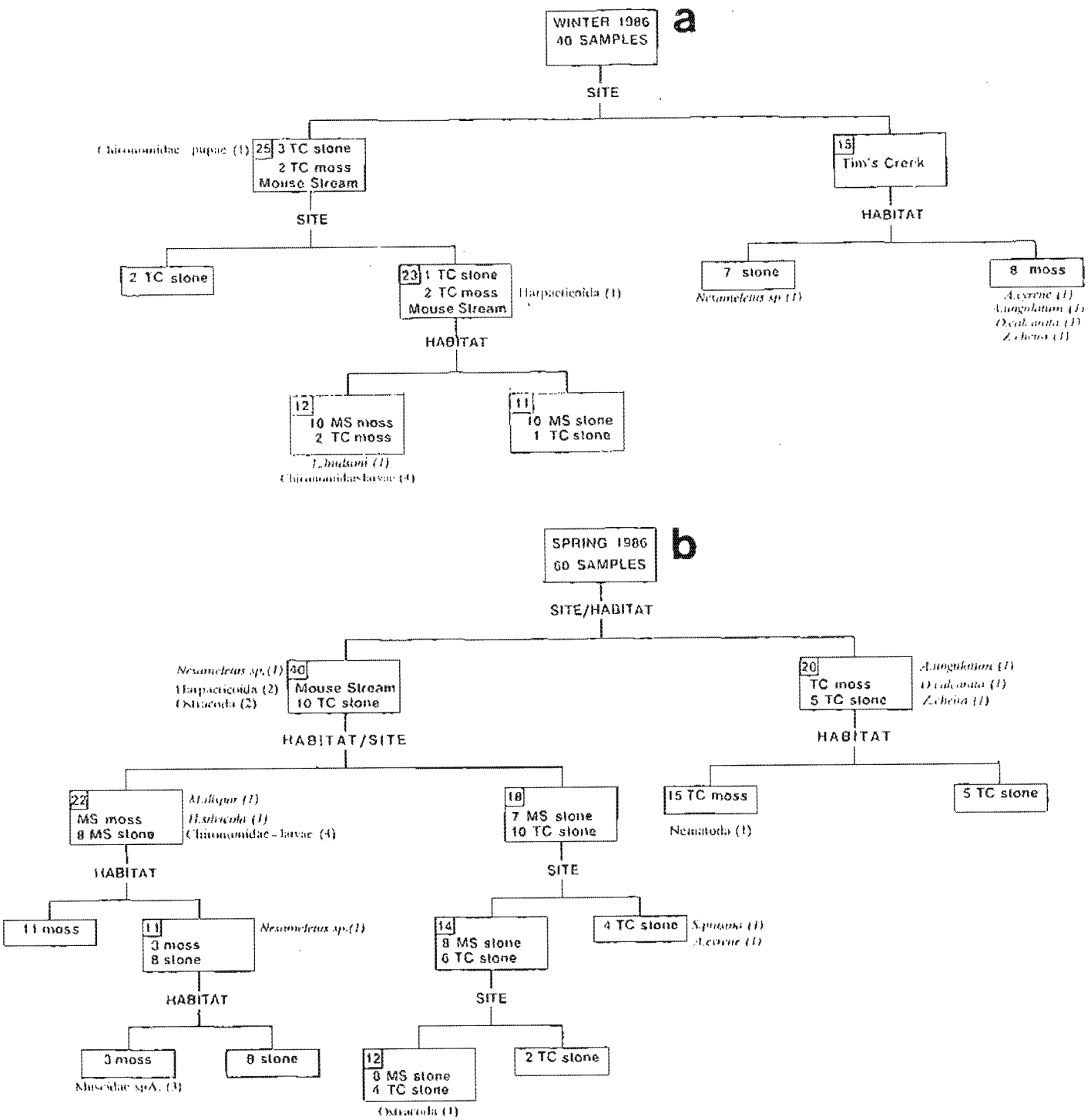
In each TWINSPAN analysis, samples were divided into smaller groups on the basis of site or habitat differences at each level (Figs 20a-f). Seasonal differences between invertebrate communities resulted in TWINSPAN dendrograms being of different lengths: all samples from spring 1987 were classified into end groups after 2 levels, whereas samples from autumn 1987 were not fully classified into end groups even after 6 levels.

Table 8: Species whose abundances were significantly ($p < 0.01$) correlated with the location of samples plotted on DECORANA axes 1 and 2. Sample aggregations on each axis could be distinguished on the basis of site or habitat differences, with aggregates from specific sites or habitats having lower or higher axis scores than others. Abundances of individual taxa were correlated with the sample scores on each axis to determine if invertebrate abundances were correlated with these scores, and by inference with particular sites or habitats. The number of seasons (maximum 6) in which a species exhibited a significant correlation is given in parentheses after its name.

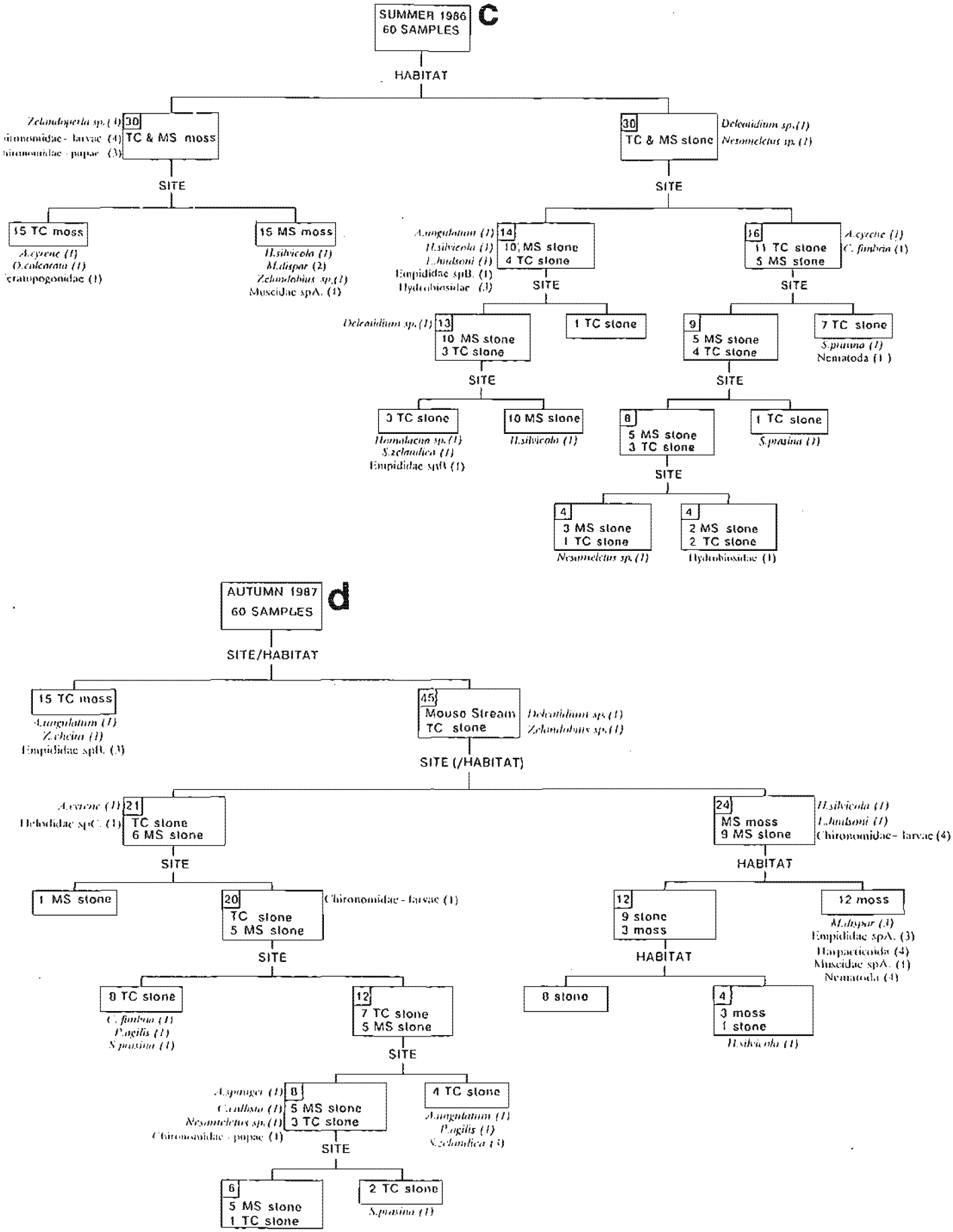
SITE DIFFERENCES		HABITAT DIFFERENCES	
MOUSE STREAM	TIM'S CREEK	BRYOPHYTES	RIFFLES
Good Indicators			
Acroperla spiniger (5) *Hydrobiosis silvicola* (5)	*Zelolessica cheira* (6) *Orchymontia calcarata* (6) *Austrosimulium ungulatum*(5) *Austroperla cyrene* (5) Empididae sp. B (5)	*Limonia hudsoni* (5) *Zelandoperla* sp. (5) Nematoda (5)	*Deleatidium* sp. (5) *Nesameletus* sp. (5) *Stenoperla prasina* (5)
Moderate Indicators			
Zelandobius sp. (4) *Macrobiotis dispar* (4) Copepoda (4) Ostracoda (4) Chironomidae-pupae (4) *Deleatidium* sp. (3) *Nesameletus* sp. (3) Hydrobiosidae (3)	Hydracarina (4) Elmidae (3)	*Hydrobiosis silvicola* (4) Muscidae sp. A (4) *Macrobiotis dispar* (4) *Zelolessica cheira* (4) Chironomidae- pupae (3) Hydrobiosidae (3) *Orchymontia calcarata* (3) Empididae sp. A (3)	Helodidae sp. C (3)
Poor Indicators			
Zelandoperla sp. (2) 9 additional taxa (1)	*Zelandoperla* sp. (2) *Halticoperla viridans* (2) *Homalaena dispersa* (2) *Philorheithrus agilis* (2) 23 additional taxa (1)	Chironomidae larvae. (2) *Acroperla spiniger* (2) Hydracarina (2) Copepoda (2) Ostracoda (2) 11 additional taxa (1)	*Oeconesus similis* (2) 15 additional taxa (1)
Total number of OTUs 20	34	27	20

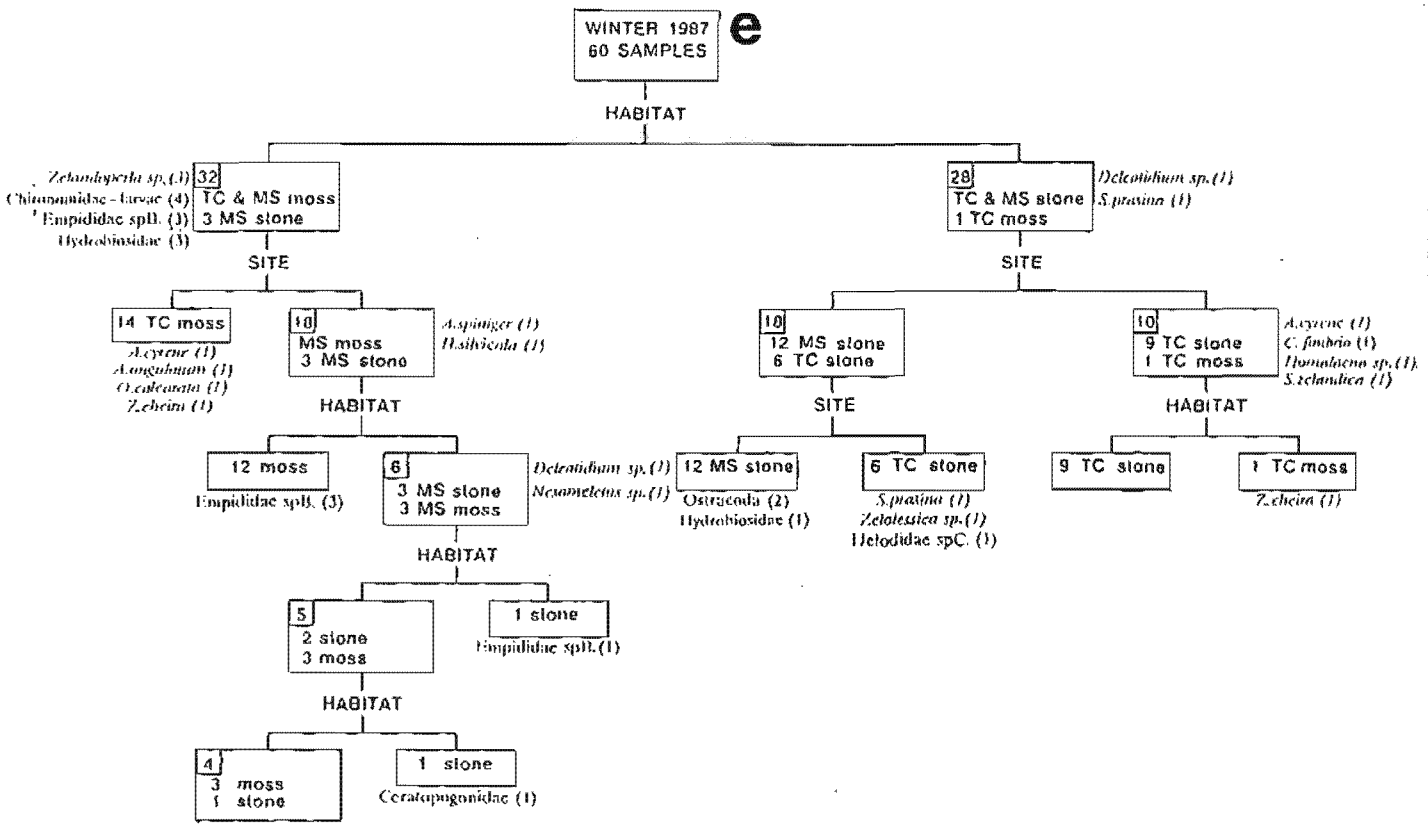
Table 9: Cumulative percentage of samples classified into discrete clusters by TWINSPAN until only seasonal differences remained in the clusters at each division.

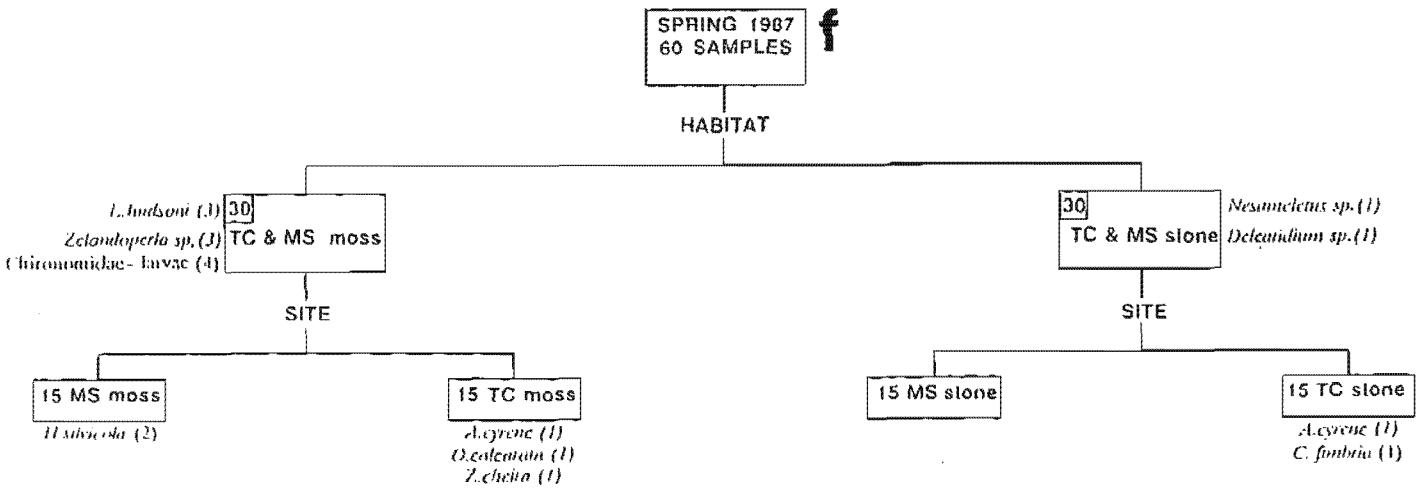
Season (number of samples)	CLASSIFICATION DIVISIONS					
	I	II	III	IV	V	VI
winter 1986 (40)	0	42.5	100			
spring 1986 (60)	0	33.3	58.2	100		
summer 1986 (60)	0	50	63.3	85.0	100	
autumn 1987 (60)	25	25	46.7	80	86.7	100
winter 1987 (60)	0	23.3	90.0	91.7	100	
spring 1987 (60)	0	100				
Average	4.2	54.8	71.6	89.2	95.6	100



Figs 20a-f: TWINSPAN classifications of samples collected monthly from bryophytes and riffles in Mouse Stream and Tim's Creek. Dendrograms show sample groupings produced by each TWINSPAN division, the number of samples in each grouping (small box) and a description of these samples (large box). At each division, the primary basis for sample separation (site, habitat, or a combination of both) is shown. Indicator pseudospecies characteristic of samples within each sample grouping are presented, showing the taxa and its pseudospecies score (parentheses; see text). Divisions were terminated when samples within a group differed only by season. Six TWINSPAN analyses were performed; a) = winter 1986, b) = spring 1986, c) = summer 1986, d) = autumn 1987, e) = winter 1987, f) = spring 1987.


SUMMER 1986
60 SAMPLES
C
HABITAT
Zelandopsyche sp.(1)
Chironomidae - larvae (4)
Chironomidae - pupae (3)
30
TC & MS moss
SITE
15 TC moss
A.cyrene (1)
O.calcarata (1)
Tanypogonidae (1)
15 MS moss
H.silvicola (1)
M.dispar (2)
Zelandobius sp.(1)
Muscidae spA. (1)
30
TC & MS stone
Deleatidium sp.(1)
Nesomicletus sp.(1)
SITE
A.angulatum (1)
H.silvicola (1)
L.hudsoni (1)
Empididae spB. (1)
Hydrobiosidae (3)
14
10 MS stone
4 TC stone
SITE
Deleatidium sp.(1)
13
10 MS stone
3 TC stone
1 TC stone
SITE
3 TC stone
Hemidactine sp.(1)
S.zelandica (1)
Empididae spB (1)
10 MS stone
H.silvicola (1)
16
11 TC stone
5 MS stone
A.cyrene (1)
C.fimbria (1)
SITE
9
5 MS stone
4 TC stone
7 TC stone
S.prasina (1)
Nematoda (1)
SITE
8
5 MS stone
3 TC stone
1 TC stone
S.prasina (1)
SITE
4
3 MS stone
1 TC stone
Nesomicletus sp.(1)
4
2 MS stone
2 TC stone
Hydrobiosidae (1)
AUTUMN 1987
60 SAMPLES
d
SITE/HABITAT
15 TC moss
A.angulatum (1)
Z.cheira (1)
Empididae spB. (3)
45
Mouso Stream
TC stone
Deleatidium sp.(1)
Zelandobius sp.(1)
SITE (/HABITAT)
A.cyrene (1)
Helodidae spC. (1)
21
TC stone
6 MS stone
SITE
1 MS stone
20
TC stone
5 MS stone
Chironomidae - larvae (1)
SITE
8 TC stone
C.fimbria (1)
P.agilis (1)
S.prasina (1)
12
7 TC stone
5 MS stone
SITE
A.sponga (1)
C.callisa (1)
Nesomicletus sp.(1)
Chironomidae - pupae (1)
8
5 MS stone
3 TC stone
4 TC stone
A.angulatum (1)
P.agilis (1)
S.zelandica (1)
SITE
6
5 MS stone
1 TC stone
2 TC stone
S.prasina (1)
24
MS moss
9 MS stone
H.silvicola (1)
L.hudsoni (1)
Chironomidae - larvae (4)
HABITAT
12
9 stone
3 moss
12 moss
M.dispar (3)
Empididae spA. (3)
Harpacticoida (4)
Muscidae spA. (1)
Nematoda (4)
HABITAT
8 stone
4
3 moss
1 stone
H.silvicola (1)


WINTER 1987
60 SAMPLES
e
HABITAT
Zelandopsyche sp.(1)
Chironomidae - larvae (4)
Empididae spII. (3)
Hydrobiosidae (3)
32
TC & MS moss
3 MS stone
28
TC & MS stone
1 TC moss
Deleatidium sp.(1)
S.prasina (1)
SITE
SITE
14 TC moss
A.cyrene (1)
A.angulatum (1)
O.calcarata (1)
Z.cheira (1)
10
MS moss
3 MS stone
A.spiniger (1)
H.silvicola (1)
HABITAT
10
12 MS stone
6 TC stone
SITE
10
9 TC stone
1 TC moss
A.cyrene (1)
C. fimbria (1)
Hamalaena sp.(1)
S.chandlica (1)
HABITAT
12 moss
Empididae spII. (3)
6
3 MS stone
3 MS moss
Deleatidium sp.(1)
Nesameletus sp.(1)
12 MS stone
Ostracoda (2)
Hydrobiosidae (1)
6 TC stone
S.prasina (1)
Zelolessica sp.(1)
Helodidae spC. (1)
9 TC stone
1 TC moss
Z.cheira (1)
HABITAT
5
2 stone
3 moss
1 stone
Empididae spII.(1)
HABITAT
4
3 moss
1 stone
1 stone
Ceratopogonidae (1)


SPRING 1987
60 SAMPLES
f
HABITAT
L.hudsoni (3)
Zelandopsyche sp.(3)
Chironomidae - larvae (4)
30
TC & MS moss
30
TC & MS stone
Nesameletus sp.(1)
Deleatidium sp.(1)
SITE
SITE
15 MS moss
H.silvicola (2)
15 TC moss
A.cyrene (1)
O.calcarata (1)
Z.cheira (1)
15 MS stone
15 TC stone
A.cyrene (1)
C. fimbria (1)

Pseudospecies analysis

At each TWINSPAN level, indicator species for the created sample groups are calculated. These indicator species were pseudospecies, which not only give an indication of what taxa are associated with each sample grouping, but also their densities. Because each group in a TWINSPAN level was made up of samples from a particular site or habitat, it was possible to determine which taxa were associated with bryophytes or riffles at in each site, and how abundant they were at each location (Table 10).

Pseudospecies were frequently associated with samples from Tim's Creek, and indeed 5 pseudospecies represented this site in three or more seasons (Table 10). In contrast, most pseudospecies at Mouse Stream were only associated with this site for only 1 or 2 seasons, with the exception of *Hydrobiosis silvicola*, which was an indicator species in 4 seasons (Table 10). The lower invertebrate densities at Tim's Creek were reflected in the TWINSPAN analysis, whereby all pseudospecies were of low abundance. In contrast five of the pseudospecies identified at Mouse Stream were of high abundance (Table 10).

More pseudospecies were indicative of bryophytes (21) than riffles (11), indicating a higher proportion of bryophyte specialists. Furthermore, more indicator species identifying bryophyte samples were high density pseudospecies, whereas all pseuodospecies from riffles were low density "taxa" (Table 10), reflecting the higher invertebrate densities in bryophytes.

Table 10: Indicator species (represented here by pseudospecies) as determined by TWINSPAN analysis of the seasonal invertebrate data. At each level in the TWINSPAN classification, samples were placed into smaller subgroups based on similarity of species composition. These subgroups consisted of samples from similar sites or habitats. The quantitative nature of the data was approximated by pseudospecies, representing abundance classes of each taxa (see text). Each pseudospecies is defined by its taxonomic name and abundance class. The number of seasons (maximum 6) in which individual taxa displayed site and habitat preferences are given in parentheses.

SITE		HABITATS	
.IOUSE STREAM	TIM'S CREEK	BRYOPHYTES	RIFFLES
Hydrobiosis silvicola 2 (4)	*Ausroperla cyrene* 1 (6)	Chironomidae larvae 4 (6)	*Nesameletus* 1 (6)
Chironomidae pupae 1 (2)	*Zelolessica cheira* 1 (5)	*Zelolessica cheira* 1 (3)	*Deleatidium* 1 (3)
Chironomidae larvae 4 (2)		*Zelandoperla* 3 (3)	
Ostracoda 2 (2)	*Austrosimulium ungulatum* 1 (4)		9 additional taxa(1)
Lacrobiotis dispar 2 (2)	*Orchymontia calcarata* 1 (4)	*Limonia hudsoni* 3 (2)	
Deleatidium 1 (2)	*Stenoperla prasina* 1 (4)	*Hydrobiosis silvicola* 3 (2)	
Hydrobiosidae 2 (2)		Empididae B 3 (2)	
Ausroperla spiniger 1 (2)	*Cristaperla fimbria* 1 (3)		
Talandobius 1 (2)		15 additional taxa (1)	
	Spaniocerca zelandica 1 (2)		
2 additional taxa (1)	*Homalaena* dispersa 1 (2)		
	12 additional taxa (1)		
Total Numbers: 21	20	21	11

DISCUSSION

The major findings of this study were the demonstration of greatly enhanced invertebrate abundances amongst bryophytes compared with riffles, and the existence of relatively discrete faunal assemblages in bryophyte and riffle habitats, both above and below the tree-line. Both sites and habitats differed with respect to temperature, water depth and velocity, and organic matter biomass, and individual taxa appeared to respond to these differences in a consistent way.

Although water chemistry differed between the two streams (Table 3), they were both characterised by very low nutrient status. Water temperature regimes were significantly different at the two sites, with Mouse Stream having less variable, but on average colder temperatures than Tim's Creek. Water depth and velocity were always shallower and faster in bryophyte habitats than riffles, and reflects the photosynthetic requirements of aquatic bryophytes for dissolved CO_2 (Bain & Proctor 1980, Allen & Spence 1981) and the distribution of stable substrates available for colonization.

In all samples, bryophytes trapped more detritus than did riffles despite the fact that their distributions were restricted to erosional areas of the stream. This highlights their ability to reduce currents within their matrices (Devantry 1987). Bryophyte biomass was also similar at the two stream sites, indicating that the reduced light intensities at Tim's Creek did not mitigate against bryophyte growth.

Seasonal and inter-site variations in biomass of LPOM, CPOM, and MPOM of bryophyte samples are largely results of sampling variability rather than natural bryophyte growth cycles. Unlike the mosses *Fontinalis antipyretica* Hedw., *Fissidens crassipes* Wils. ex Bry. Eur. and *Amblystegium riparium* (Hedw.) Br.Eur. which exhibit a significant winter decline in biomass in English rivers (Wehr 1983, Kelly & Whitton, 1987), all bryophytes in my study were present year round.

Although quantities of allochthonous detritus (FPOM) trapped by the plants differed seasonally (pers. obs), this trapped material constituted only a small percentage of organic matter weight and would not have greatly influenced seasonal biomass patterns of bryophytes.

Quantities of organic matter in riffle areas were similar at both sites, although there were probably greater allochthonous inputs at Tim's Creek, given the nature of its riparian vegetation. Although energy inputs to forested streams are generally thought to be predominantly from allochthonous material (e.g., Fisher & Likens 1973, Sedell *et al.* 1974, Conners & Naiman 1984, King & Cummins 1989), the physical instability of many New Zealand streams reduces organic matter retention (Winterbourn 1986, Graesser 1988). Riffle areas retained an average of 57 and 74 g AFDW m^{-2} at Mouse Stream and Tim's Creek, slightly higher than that observed in four streams in South Westland (15 - 26 g AFDW m^{-2}, Graesser 1988), but much lower than benthic organic matter values recorded in more stable streams (e.g., 496 and 108 g AFDW m^{-2} in two seasons at Middle Bush Stream, Cass (Rounick & Winterbourn 1982)).

High levels of trapped FPOM within bryophyte mats are a consequence of the environmental stability and current-reducing velocities characteristic of these plants (Glime 1972, Johnston 1978, Smith-Cuffney 1987). Bryophytes at Mouse Stream trapped more FPOM than bryophytes at Tim's Creek, even though FPOM inputs at the latter were apparently higher. This may reflect the observed thicker and deeper mat morphology of the mosses at Mouse Stream which may therefore have greater detrital entrapping "efficiencies" than the more loosely arranged liverworts at Tim's Creek. Furthermore, abrasion of bryophyte leaves by waterborne particles is known to destroy the lower (and older) leaves of *Fontinalis antipyretica* (Glime & Conboy 1971). A similar loss of older leaves was observed for the liverworts *Plagiochila retrospectans* and *Hepatostolonophora paucistipula* at Tim's Creek and may have further reduced their detrital trapping efficiency.

Invertebrate communities associated with aquatic bryophytes have been reported to have either greater taxonomic richness than those on adjacent stony substrata (e.g., Cowie & Winterbourn 1979, McKenzie-Smith 1987, Brusven *et al.* 1990), or no apparent increase in richness (e.g., Hynes 1961, Egglishaw 1969, Thorup & Lindegaard 1977). I found that invertebrate densities were up to ten times greater among bryophytes than in stony riffles, and in this respect they were comparable to the

findings of Hynes (1961) and Brusven *et al.* (1990) who respectively found 6 and up to 7 times more invertebrates in bryophytes than riffles.

The presence of greater invertebrate densities among bryophytes has often been attributed to an increased in surface area available for colonization (Minshall 1984), and it is well known that invertebrates frequently respond positively to increases in macrophyte surface area in a variety of aquatic environments (Krecker 1939, Wieser 1952, Rosine 1955, Harrod 1964, Rooke 1984, 1986). However, even when abundances of invertebrates associated with the liverwort *Lophocolea planiscula* in a Victorian (Australia) upland stream were corrected for the surface area of the plant, they were still greater than those in riffles (McKenzie-Smith 1987), indicating that density attained is not solely a response to surface area availability.

Likewise, morphologically complex habitats of other kinds often support more species and numbers of aquatic invertebrates than simple areas (e.g., Hart 1978, Erman & Erman 1984, Tokeshi & Pinder 1985, Rooke 1984, Dean & Connell 1987a, 1987b) although this is not always the case (Russo 1990). Because bryophytes enhance periphyton colonization and detritus entrapment (Johnson 1978, Smith-Cuffney 1987, this study, Chapter 7), a heterogeneous substratum consisting of algae, detritus and bryophyte is created in an environment of reduced current velocity. Its greater complexity and stability compared with that of bare streambed materials therefore contribute to the increased abundances of animals there.

In addition to enhancing habitat complexity and stability, bryophytes also provide invertebrate colonisers with three potential foods: the plants themselves, trapped detritus and algae. While numerous reports of aquatic bryophyte herbivory exist (e.g., Byers 1961, Erichsen-Jones 1969, Fuller & Stewart 1977, Williams & Williams 1982, Mutch & Pritchard 1984a,b, Willoughby & Mappin 1988, Wyatt & Stoneburner 1989), there is a general consensus that consumption is less than expected, especially given the taxonomic diversity of bryophyte dwelling invertebrates (Frankland 1974, Gerson 1972, Lawrey 1987). Although larvae of the tipulid *Limonia hudsoni* consume fresh bryophyte tissue (Chapter 6), most of the invertebrates associated with these plants consumed trapped detritus and algae. The enhanced invertebrate densities

may thus reflect consumption of this often abundant food, and not of the bryophyte itself.

Invertebrate densities were consistently higher amongst bryophytes and riffles at Mouse Stream than at Tim's Creek. Although instability of bed materials reduces organic matter retention capacity in New Zealand streams (Collier & Winterbourn 1987, Collier 1988, Graesser 1988), this can only help explain the lower abundances in riffles at Tim's Creek. Bryophytes at this site represent highly stable habitats within a generally unstable stream environment, yet invertebrate densities within these plants were lower than at Mouse Stream. The presence of higher invertebrate densities among bryophytes and riffles at Mouse Stream may be a consequence of greater associated algal biomass at that site (Chapter 7), and indeed algal biomass has been implicated in explaining higher invertebrate densities in open streams (Murphy & Hall 1981, Behmer & Hawkins 1986, Smith-Cuffney 1987, Feminella *et al.* 1989).

With regard to particular taxa, various species of Chironomidae have been noted as dominant colonists of bryophytes in several studies (e.g., Percival & Whitehead 1929, Hynes 1961, Glime 1968, Stern & Stern 1969, Cowie & Winterbourn 1979, Brusven *et al.* 1990) including the present one, although amphipods have been reported as dominants in other studies (e.g., Thorup & Lindegaard 1977, McKenzie-Smith 1987, Chadderton 1990).

Nematodes, crustaceans (harpactacoid copepods and ostracods) and tardigrades were also abundant among bryophytes in this study, as observed also by Cox (1988), who investigated the fauna associated with *Eurhynchium riparioides* (Hedw.) Rich and *Fontinalis novae-angliae* Sull. in two second-order streams in Tennessee, U.S.A. However, he found that bdelloid rotifers were the most abundant taxonomic group, and they were also reported to be common on bryophytes by Edmonson (1944), Pennak (1950), Zullini & Ricci (1980), Gerson (1972) and Evans (1984). Despite the fact that I counted invertebrates on only a 250 µm mesh sieve, rotifers comprised less than 0.001% of total invertebrate numbers in this study, whereas other members of the meiofauna of similar sizes (e.g., nematodes and tardigrades) were considerably more abundant (see also Chapter 3).

Although chironomid larvae were also numerically dominant in stony riffles at both of my sites, abundances of *Deleatidium* and *Zelandoblus* were much higher. Absence of larval *Deleatidium*, *Nesameletus* and *Stenoperla prasina* from bryophytes may reflect their inability to move freely among bryophyte leaves and stems without damaging their lateral abdominal gills. Similar observations of the absence of wide bodied taxa with external abdominal gills from bryophytes were made by Percival & Whitehead (1929, 1930) and (Brusven *et al.* 1990).

Finally, multivariate analyses illustrated that bryophytes not only enhance invertebrate abundance but also support communities of distinctive taxonomic composition. Ordination of samples separated them into specific site and habitat groupings on the basis of species similarity, and divisions were also made on this basis by TWINSPAN classification.

While very little is known of invertebrate communities associated with bryophytes in other New Zealand streams, the high frequency of occurrence of a gripopterygid stonefly, *Zelandoperla* sp., the helicophid caddis *Zelolessica cheira* and an empidid fly (Empididae sp.B) in bryophyte samples at Tim's Creek, supports the observation by Cowie (1975) and Cowie & Winterbourn (1979) that they are characteristic inhabitants of bryophytes.

Close associations between invertebrates and bryophytes are related to the use of the plant for case construction and/or shelter during pupation (Appendix 4) or as food where either the bryophyte itself, or the associated detritus and periphyton is consumed (Chapter 6). In addition, the plants serve as refugia from strong currents, especially during periods of high discharge.

CONCLUSIONS

Streams in Arthur's Pass National Park are greatly influenced by the mountainous topography, steep catchments and heavy, unpredictable rainfall of the area. These factors result in highly variable water discharge and often extensive substratum movement. Within the streams, bedrock areas or large, buried boulders are often

extensively covered by bryophytes. They form permanent patches of substrata that offer high stability in an environment otherwise characterised by high physical instability.

Bryophytes often support extensive growths of periphyton and trap greater quantities of fine detritus than adjacent riffles. This is thought to partially explain their greatly increased invertebrate densities.

A number of taxa seem to show habitat preference for bryophytes, including nematodes, chironomids, the cranefly *Limonia hudsoni*, an empidid fly (Empididae sp. B), a stonefly *Zelandoperla* sp., the caddisflies *Zelolessica cheira* and *Hydrobiosis silvicola*, and the tardigrade *Macrobiotis dispar*. These taxa utilise bryophytes in a variety of ways including direct consumption by *Limonia* larvae (Chapter 6), shelter from currents by tardigrades and nematodes, and consumption of associated detrital and periphytic material by chironomids and *Zelandoperla*. Other taxa, e.g., the larvae of *Deleatidium*, *Nesameletus* and *Stenoperla prasina* appear unable to penetrate the tightly entwined bryophyte stems and are found only in stony sections of stream bed. These points are elaborated upon in subsequent chapters of this thesis.

CHAPTER THREE:

MEIOFAUNAL COMMUNITIES ASSOCIATED WITH AQUATIC BRYOPHYTES IN TWO NEW ZEALAND ALPINE STREAMS

INTRODUCTION

Aquatic bryophytes are often a conspicuous feature of New Zealand alpine streams, and occur on immobile boulders and bedrock. They provide many invertebrates with a stable, permanent habitat in streams characterised by frequent periods of high discharge and substrate instability. Despite the presence of often extensive bryophyte growths in first order streams, little is known about their associated invertebrate communities. Cowie & Winterbourn (1979) examined the invertebrate assemblages associated with bryophytes in a sub-alpine spring-brook at Cass, and macroinvertebrate associations with bryophyte and gravel substrata has been examined in two alpine streams in Arthur's Pass National Park (Suren 1990, 1991). No other studies however have focussed on invertebrate and bryophyte associations in New Zealand.

Previous investigations of invertebrates associated with bryophytes have concentrated particularly on insects (e.g., Percival & Whitehead 1929, 1930, Hynes 1961, Gilme 1968b, Thorup & Lindegaard 1977, Maurer & Brusven 1983, Smith-Cuffney 1987, Brusven *et al.* 1990). Nevertheless, an often overlooked aspect of benthic invertebrate communities, and in particular those associated with bryophytes, is the meiofauna (O'Doherty 1985, Rundle & Hildrew 1990). This consists of microcrustaceans, nematodes, rotifers, tardigrades and small larval insects. While a few studies have examined lotic microinvertebrates (e.g., Williams & Hynes 1974, Jones 1986, Shiozawa 1986, Williams 1989, Rundle & Hildrew 1990), a study by Cox (1988) in two streams in Tennessee, U.S.A., represents the only work investigating meiofaunal communities associated with bryophytes.

Lotic meiofaunal taxa are often hyporheic (Williams & Hynes 1974, Shiozawa 1986, Williams 1989) and therefore they are unlikely to occur in places where current velocity is high. They are often found in silt laden environments characterised by slow flowing laminar water with thick boundary layers, or in the case of hyporheos, in erosional habitats where silt deposition is low (Shiozawa 1986). Although aquatic bryophytes occur in areas of high water velocity, they often trap large quantities of detritus among their stems. This greatly increases spatial heterogeneity of otherwise relatively homogeneous rock faces, and results in the formation of depositional, low current velocity microhabitats (Gilme & Clemons 1972, Johnson 1978, Devantry 1987). These changes to the stream microenvironment attract members of the meiofaunal community to bryophytes. Here they may dwell amongst stems of the plant, behaviour that is comparable to that of dwelling between interstices of substratum particles in the hyporheos.

In New Zealand, our knowledge of aquatic meiofauna is limited primarily to taxonomic and ecological investigations of lake faunas (Chapman & Lewis 1976). In the present study, I examined the meiofauna associated with bryophytes in 2 alpine streams in Arthur's Pass National Park. Base-line data on faunal composition of New

Zealand meiofauna are presented together with community composition and population changes in bryophyte and riffle habitats over a 6 month period.

MATERIALS AND METHODS

1. Field Sampling

As part of an intensive investigation of invertebrate communities associated with bryophytes, five replicate Surber samples were taken monthly from bryophytes and stony riffles at each site from July 1986 to January 1988. Meiofauna (animals <250 µm) were sorted from samples taken in the last 6 months of 1987, and provide the basis of this faunal account.

Bryophytes covering flat rocks were scraped with a razor blade into a 0.01 m^2 Surber sampler (100 µm mesh). Stony riffles were sampled to a depth of 10 - 15 cm with a second Surber sampler (area= 0.02 m^2, 100 µm mesh) which had a foam flange (3 cm thick) around its base to ensure a firm seal with the substratum. Plant material adhering to stones was removed with a nylon brush and added to each collection. Water velocity at the upstream right and downstream left-hand sides of the sample area was measured with a current meter (Nixon Instrumentation Limited) with the probe resting 5mm from the substratum surface.

2. Sample Preparation and Analysis

All samples were frozen (-18°C) 3 to 6 hours after collection. After thawing, organic material in riffle samples was separated from stones and gravel by elutriation. Organic material was passed through nested sieves (2.0mm, 1.0mm, 500 µm, 250 µm, 60 µm) and processed as described previously (Chapter 2).

Invertebrates collected on the 60 µm sieve consisted primarily of small non-insect taxa. While some of them were retained by the 250 µm mesh, and larger sieves, most were present on the smallest mesh. Chironomid larvae, however, were present in similar densities on each sieve, although only first instar larvae were trapped by the 60 µm sieve. Because the definition of "meiofauna" is essentially arbitrary, I did not restrict my analysis to individuals less than a certain size but included all individuals of selected taxa present on all sieves. Taxa considered were those present on the 60 µm and 250 µm sieves in at least 2 months, irrespective of site or habitat.

All material collected on the 60 µm mesh sieve was subsampled with a quadripartite splitter and, depending on the amount of detritus present, one subsample or part of it was examined in a small Bogorov tray (channel width 7 mm) at magnifications up to times 150 (Chapter 2).

Following removal of invertebrates, all remaining organic matter on each sieve was dried at 60°C (48 h), weighed and ashed in a muffle furnace (550°C, 12 h) to determine ash-free-dry-weight (AFDW). Material on each sieve corresponded to large,

coarse, medium, fine and ultra-fine particulate organic matter (LPOM, CPOM, MPOM, FPOM, and UFPOM), respectively. Organic matter data collected thus represented different sized fractions of all material trapped in riffle areas, and total biomass of bryophytes, accumulated detritus and periphytic algae in bryophyte samples. Previous analysis (Chapter 2) had shown that the FPOM fraction in bryophyte samples was predominantly detritus (making up <10% of total weight): the UFPOM fraction in bryophyte samples also represented trapped material.

3. Statistical Analysis

Previous analyses (Chapter 2) indicated that significant differences in water temperature, depth and velocity, and AFDW of 4 organic matter size fractions (LPOM, CPOM, MPOM, and FPOM) occurred between sites and habitats. Data on detritus trapped by bryophytes (i.e., organic matter retained on the 250 and 60 µm mesh sieves (FPOM and UFPOM)), taxonomic richness and invertebrate abundance were used in the present inter-site and inter-habitat comparisons. Split-plot ANOVAs following $\log_{10}(x+1)$ transformation were carried out using time, site and habitat as treatments (Sokal and Rohlf 1981).

Invertebrate abundance data were analysed by DECORANA (Hill 1979a) on PC-Ord software (See Chapter 2) and values for all environmental parameters measured were regressed against DECORANA axes (*as per* Rundle and Hildrew 1990). Correlations between the abundance of individual taxa and sample scores on each DECORANA axis were calculated to determine which taxa were significantly correlated with particular site/habitat aggregations.

Samples were also classified by TWINSPAN as previously described (Chapter 2) with the quantitative nature of the data approximated by creation of pseudospecies (Gauche 1986, McCune 1987, Marchant 1990, Rundle and Hildrew 1990). Pseudospecies cut levels, were set at 0, 1, 2, 3, 4 and 5, corresponding to densities of each taxon of 0, 10, 100, 1 000, 10 000 and 100 000 individuals m^{-2}. I pooled monthly data to form two groups for analysis; "winter" samples (June-August) and "spring" samples (September-November).

RESULTS

Organic matter

Riffles at each site trapped similar quantities of FPOM and UFPOM ($t= 0.35$, FPOM; 0.33, UFPOM, $p>0.05$; $x= 8.4$ and 3.9 g m^{-2} at Mouse Stream; $x= 8.0$ and 2.9 g m^{-2} at Tim's Creek). Bryophytes at each site also trapped similar quantities of FPOM ($t= 1.49$, $p>0.05$; $x= 19.5$ g m^{-2} at Mouse Stream; $x=13.8$ g m^{-2} at Tim's Creek) but those at Mouse Stream contained significantly more UFPOM than those at Tim's Creek ($t= 3.23$, $p<0.005$; $x= 16.9$ g m^{-2} at Mouse Stream; $x= 7.1$ g m^{-2} at Tim's Creek). At both sites, bryophytes trapped

more FPOM and UFPOM than riffles (F= 22.34, 38.76, respectively; p<0.001). Although quantities of trapped detrital material fluctuated over time (Figs 1,2), clear temporal changes were not found.

The meiofauna

Taxonomic richness

The meiofauna collected at the 2 sites comprised 22 operational taxonomic units (OTUs) (Table 1). Aquatic mites (11 taxa), Chironomidae and Nematoda were the most diverse taxonomic groups. Numbers of OTUs in samples varied from month to month but were greater at Mouse Stream than Tim's Creek (x= 8.4 OTU at Mouse Stream; x= 7.8 OTU at Tim's Creek; F= 4.50, p<0.05). Riffles and bryophytes supported similar numbers of OTU in both streams.

Community composition: percentage contribution of taxa

Chironomid larvae were the most abundant taxa in all samples combined (46.3%), followed by nematodes (18.2%), copepods (16.7%) and ostracods (3.7%) (Fig. 3). Abundances of the aquatic mite *Paratryssaturus* and the tardigrade *Macrobiotis dispar* Murray contributed 3.1% and 2.1%, respectively to the total population. Densities of other taxa (rotifers and other aquatic mites) contributed less than 1% of invertebrate density. Bryophyte samples were dominated by chironomids, which contributed more to invertebrate density at Tim's Creek than at Mouse Stream (Fig. 3), where they were numerically more abundant.

Similarly, riffle meiofaunas were dominated by chironomids, although ostracods were the second most abundant OTU at Mouse Stream in contrast to copepods at Tim's Creek (Fig. 3). At both sites, mites were relatively more abundant in riffles than amongst bryophytes, whereas rotifers were absent from riffles.

Invertebrate densities

Total invertebrate densities within both habitats in the two streams fluctuated significantly throughout the sampling period (F= 2.44 p<0.05). Little pattern existed in these fluctuations and densities at Mouse Stream peaked at 1.1 million animals per m^{-2} in April (Fig. 4a); maximal densities at Tim's Creek (0.16 million animals per m^{-2}) occurred in October (Fig. 4b). Average meiofaunal densities in both bryophyte and stony riffle samples from Mouse Stream were always significantly higher than at Tim's Creek (F= 28.66, p<0.001; x= 2.92×10^5 and x= 6.24×10^4 individuals m^{-2} of streambed at Mouse Stream and Tim's Creek, respectively) Furthermore, bryophytes always supported more animals per unit area of streambed than stony riffles at both sites (F= 29.16, p<0.001; x= 3.39×10^5 and x= 1.54×10^4 individuals m^{-2} of bryophyte and riffle habitat).

Densities of chironomids, nematodes, copepods and tardigrades all peaked in August at Mouse Stream, whereas densities at Tim's Creek fluctuated without apparent

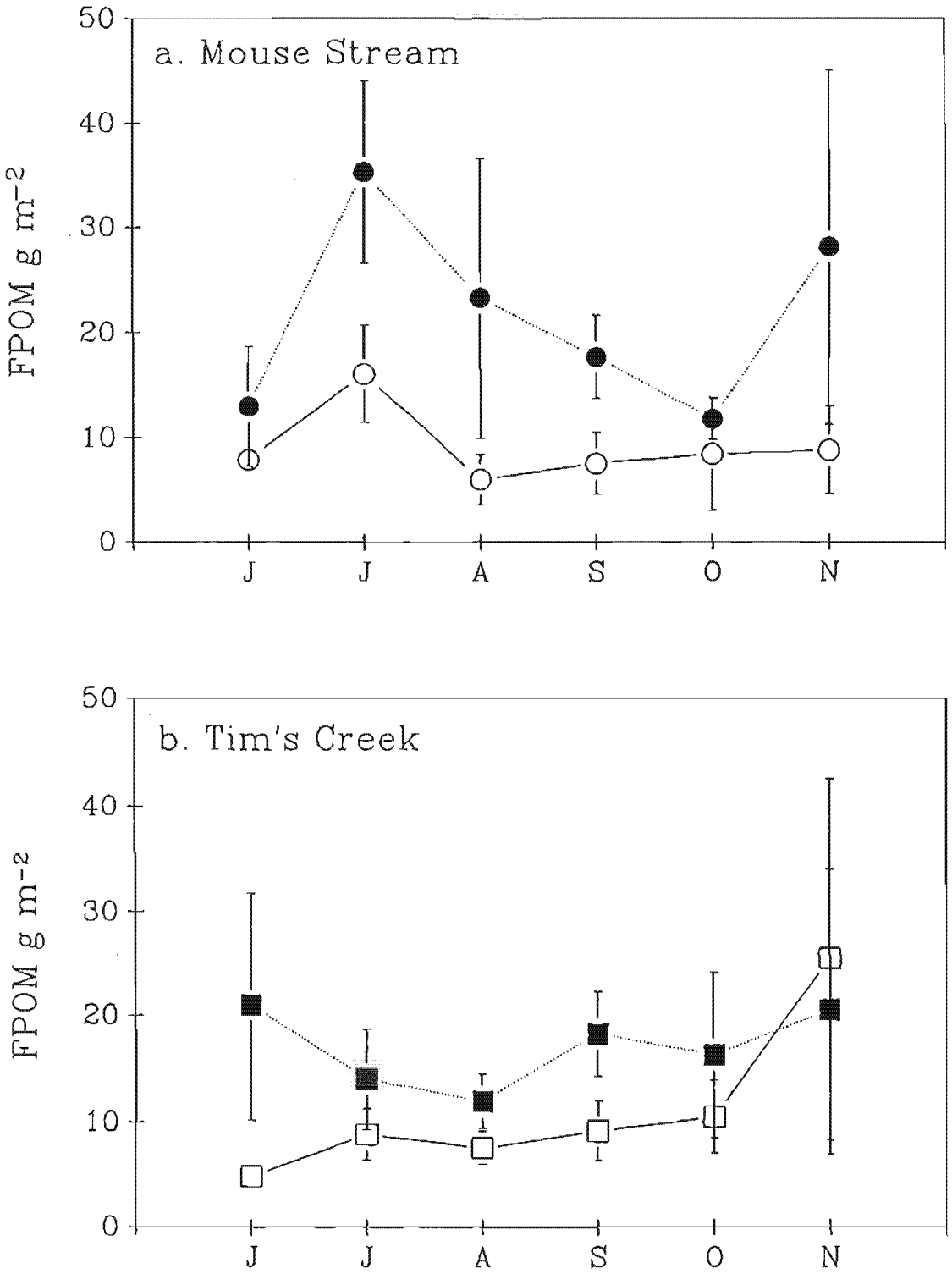


Fig. 1: Quantities of trapped fine detritus (FPOM, retained on a 250 μm mesh sieve) in bryophyte and riffle habitats: a = Mouse Stream; b = Tim's Creek. Open symbols represent samples from riffles; closed symbols represent samples from bryophytes; ($x \pm 1SE$, $n = 5$). Error bars associated with some samples are encompassed by the symbol.

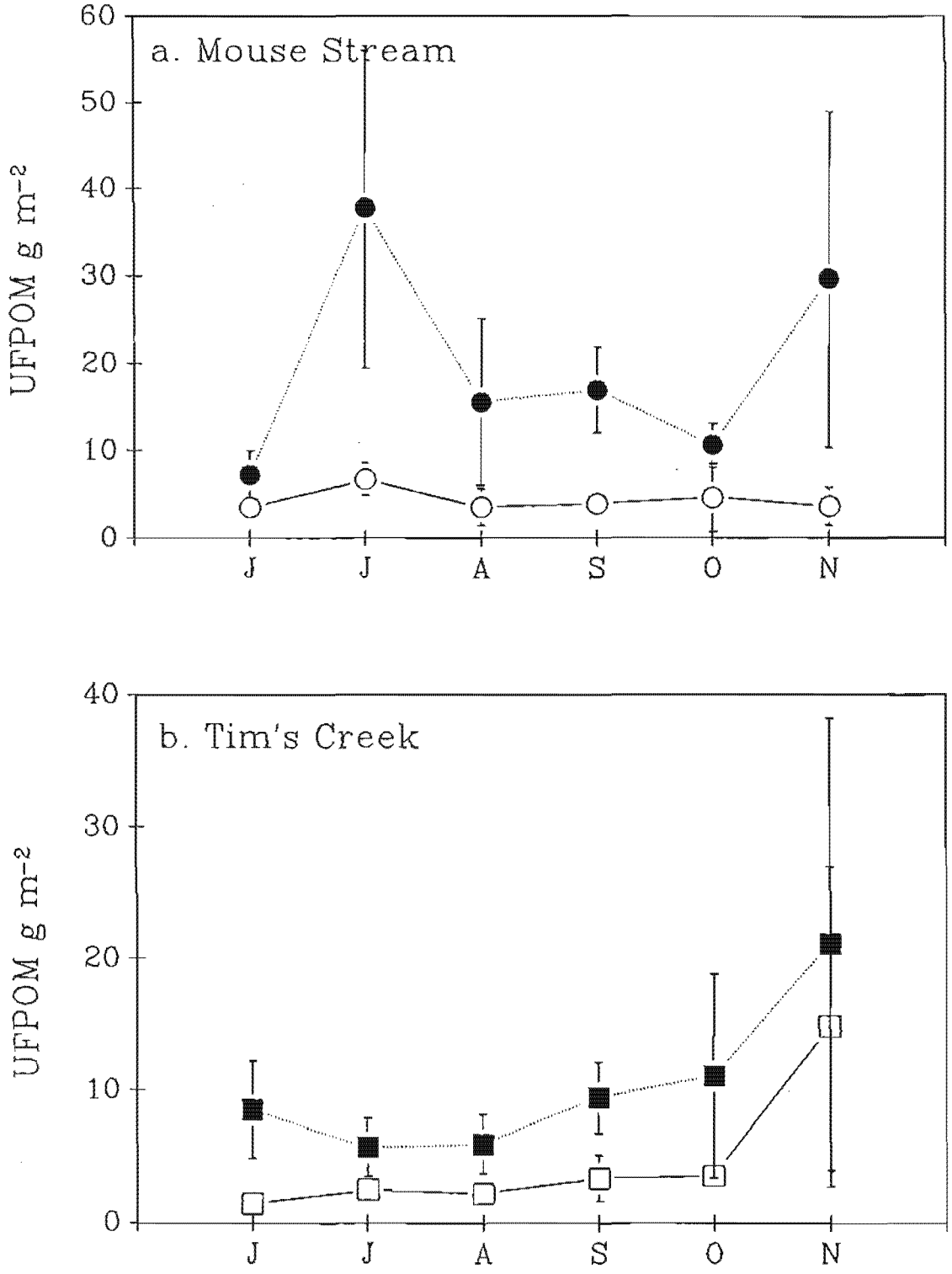


Fig. 2: Quantities of trapped ultrafine detritus (UFPOM, retained on a 60 µm mesh sieve) in bryophyte and riffle habitats. Conventions as per Fig. 1.

Table 1: Taxonomic list of meiofauna collected from Mouse Stream and Tim's Creek and retained on a 60µm mesh sieve. The suborder harpacticoida were identified to species where possible by Dr. R. Hamond, but was treated as 1 OTU for the quantitative analysis. (MS and TC in parenthesis indicate presence at Mouse Stream and Tim's Creek respectively).

Phylum Rotatoria
Class Digonota
Order Bdelloidea (MS, TC)

Phylum Nematoda
Phylum Tardigrada
Class Eutardigrada
Order Macrobiotoidae
Family Macrobiotidae
Macrobiotis dispar Murrary (MS, TC)

Phylum Arthropoda
Class Crustacea
Subclass Copepoda

Order Eucopepoda
Suborder Harpacticoida
Family Canthocamptidae
Canthocamptus ?howardorum (MS)
Canthocamptus ?maoricus (TC)
Attheyella stillicidarum Lewis (MS,TC)
A. cf *brehmi* (TC)
Antarctobiotus elongatus Lewis (MS,TC)
A. cf *diversus* (TC)
Subclass Ostracoda
Order Podocopa (1 genus; MS, TC)

Class Insecta
Order Diptera
Family: Chironomidae (several genera; MS,TC)

Class Arachnida
Order Acarina
Family Anisitsiellidae
Anisitsiellides sp. A (MS,TC)
A. sp. B (TC)
Family Aturidae
Paratryssaturus sp. (MS,TC)
Pseudotryssaturus acutus Cook (TC)
Family Hydryphantidae
Euwandesia sp. (MS,TC)
Family Hygrobatidae
Zelandobatella naias Hopkins (TC)
Family Momoniidae
Neomomonia sp. (MS, TC)
Unidentified Acarina larvae; sp.A

Order Oribatida
Several genera; sp. A
sp. B

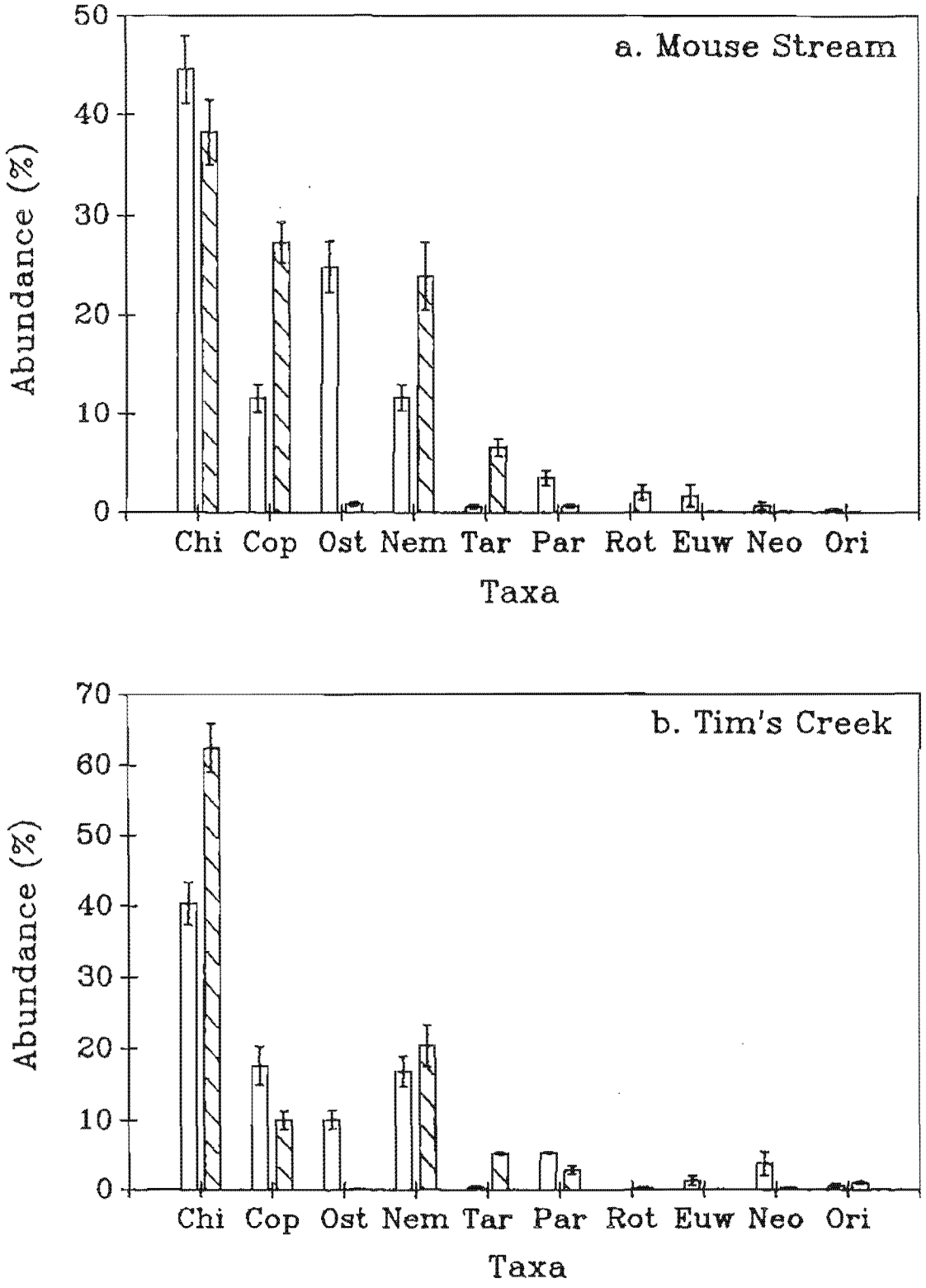


Fig. 3: The percentage contribution of individual taxa to total meiofaunal abundance within each habitat: a= Mouse Stream; b= Tim's Creek. Open bars represent samples from riffles; striped bars represent samples from bryophytes ($\bar{x} \pm 1SE$, n=5). X - axis notations: Chi = Chironomidae; Cop = Copepoda; Ost = Ostracoda; Nem = Nematoda; Tar = Tardograda; Par = *Paratryssoturus* sp; Rot = Rotifera; Euw = *Euwandesia* sp; Neo = *Neomomonia* sp; Ori = Oribatida sp A.

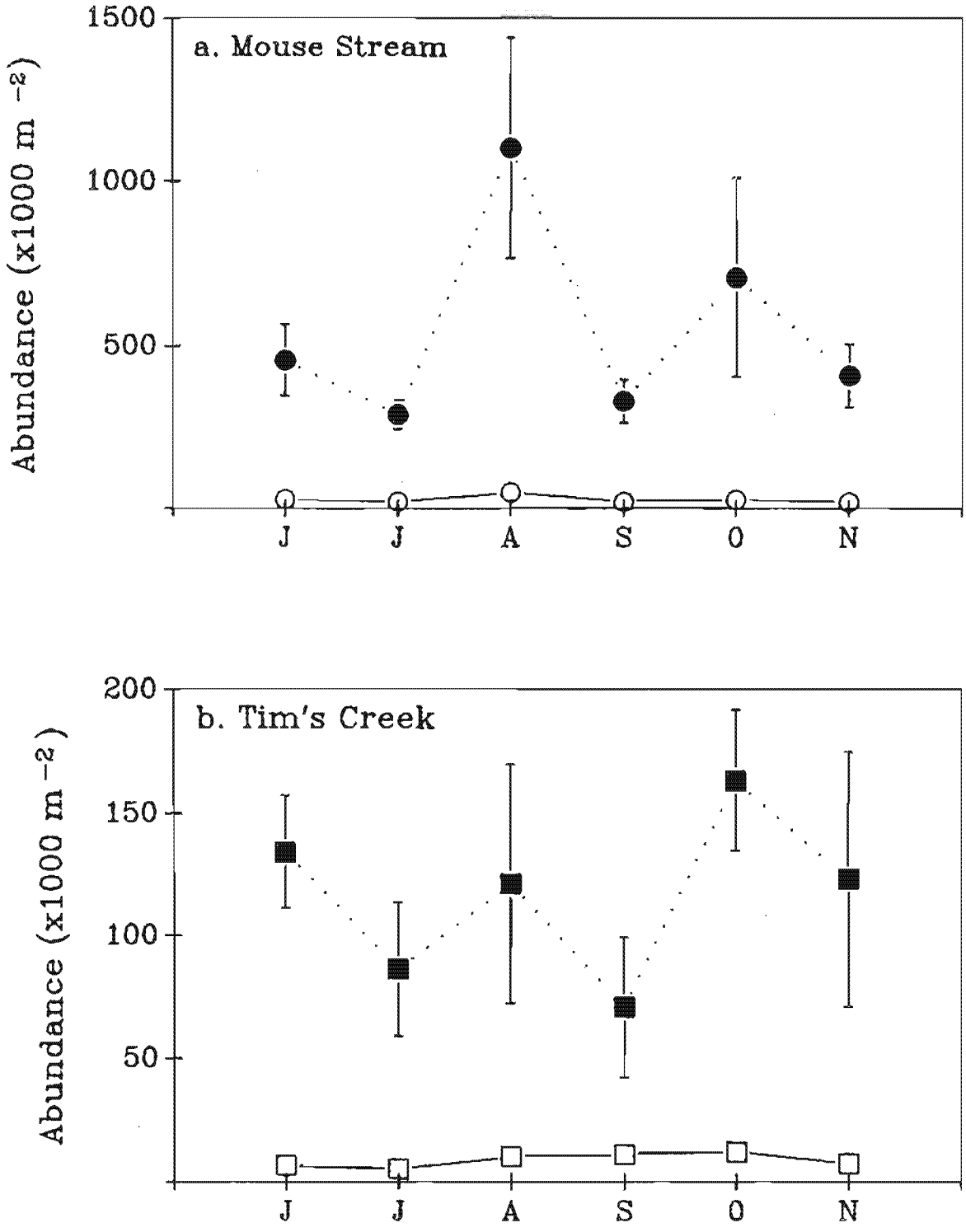


Fig. 4: Total abundance of meiofauna associated with bryophytes (closed symbols) and riffles (open symbols) at a, Mouse Stream; b, Tim's Creek; (x ± 1 SE, n = 5). Error bars associated with some data points are encompassed by the symbol.

patterns (Figs 5-8). Densities of these taxa were significantly ($p<0.0001$) greater on bryophytes than in riffles, and their densities were always significantly ($p<0.0001$) higher in Mouse Stream than Tim's Creek.

In contrast, ostracods were often more abundant in stony riffles than on bryophytes (Figs 9a,b). Ostracod densities at Mouse Stream peaked in August, and were also high in October, and were higher in bryophytes only in July. Ostracod densities at Tim's Creek were always higher in riffles (Fig. 9b). Bdelloid rotifers were more abundant among bryophytes at Mouse Stream than at Tim's Creek, and were absent from riffles at both sites (Fig 10).

Densities of aquatic mites were usually higher ($p<0.001$) on bryophytes at Tim's Creek (Figs 11-13), although those of *Anisitsiellides* sp.A (Anisitsiellidae) and an oribatid (sp. 1) were highest on bryophytes at Mouse Stream in August (Figs 11-12). Densities of *Paratryssaturus* on bryophytes at Mouse Stream increased over time whereas in riffles they decreased over time (Fig. 13).

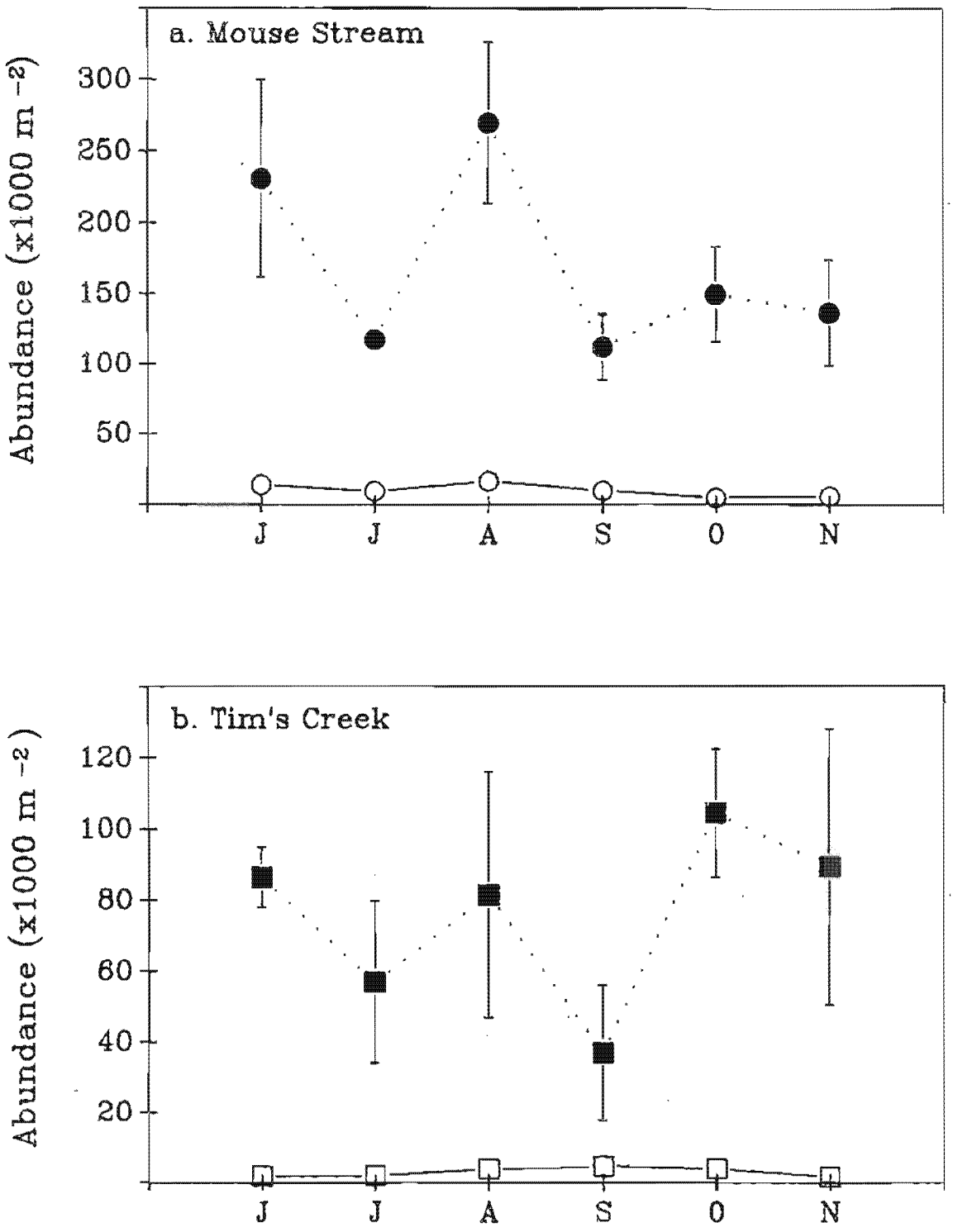


Fig. 5: Abundance of Chironomidae associated with bryophytes (closed symbols) and riffles (open symbols) at a, Mouse Stream; b, Tim's Creek; (x ± 1 SE, n = 5). Error bars associated with some data points are encompassed by the symbol.

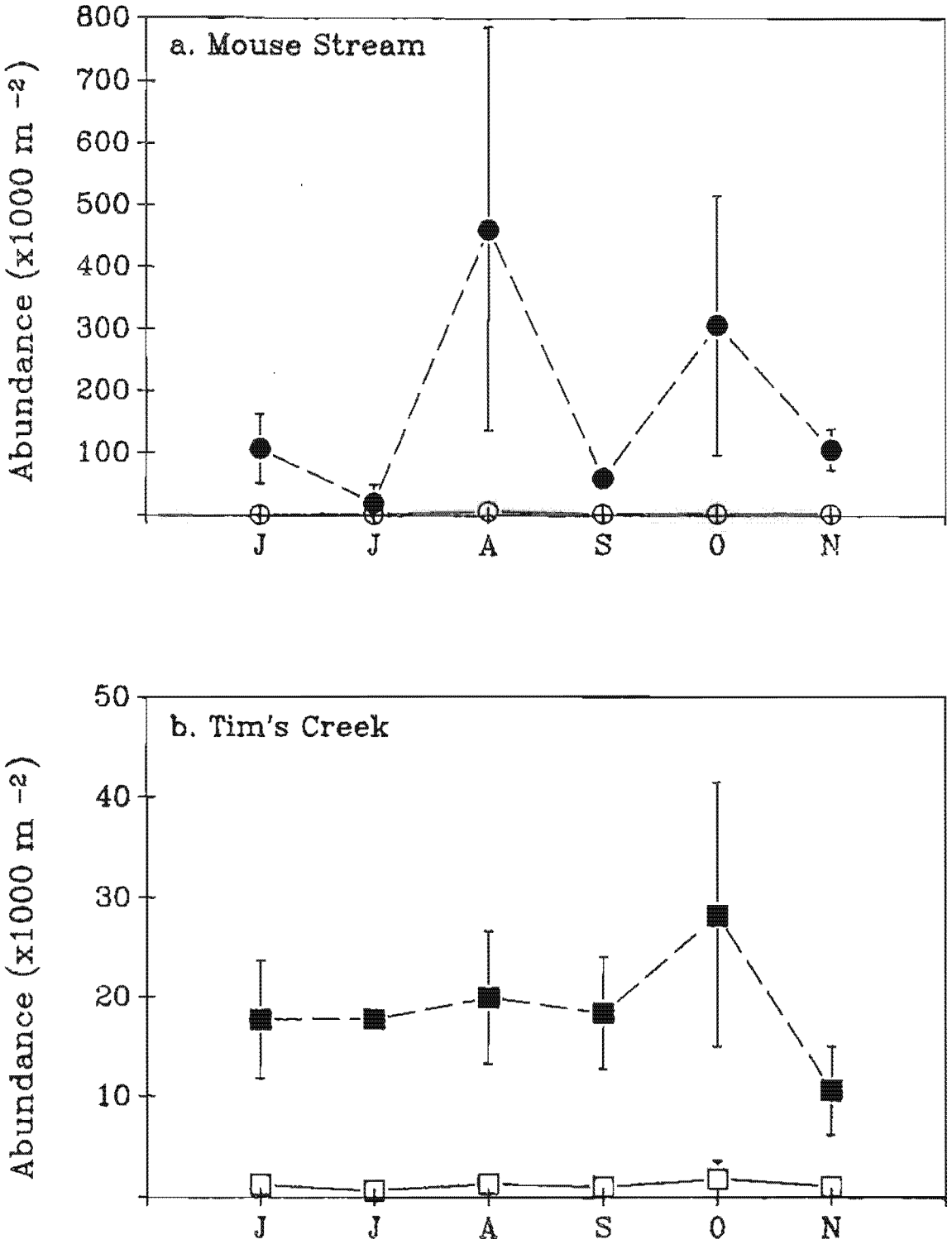


Fig. 6: Abundance of Nematoda associated with bryophytes (closed symbols) and riffles (open symbols) at a, Mouse Stream; b, Tim's Creek; (x ± 1 SE, n = 5). Error bars associated with some data points are encompassed by the symbol.

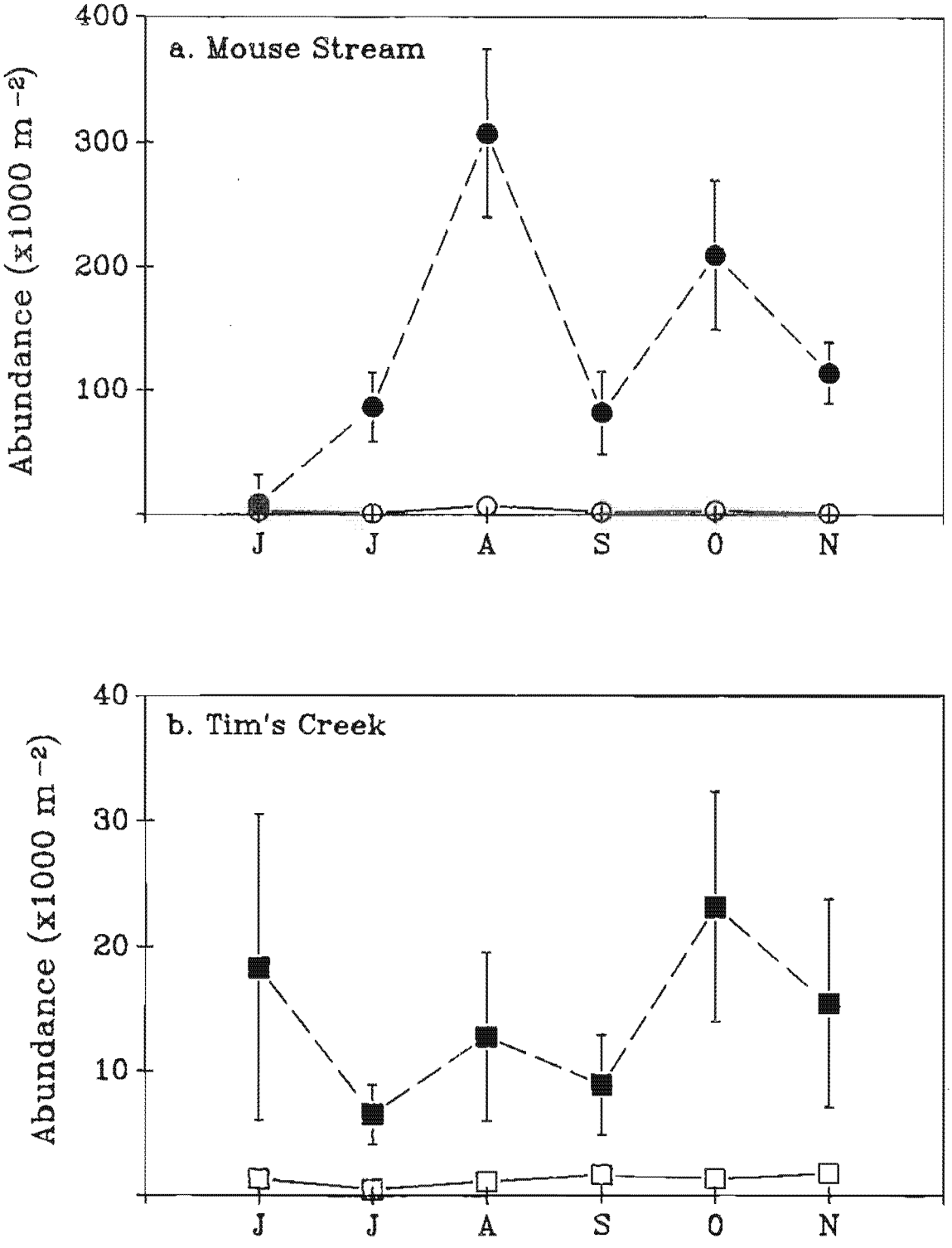


Fig. 7: Abundance of Copepoda associated with bryophytes (closed symbols) and riffles (open symbols) at a, Mouse Stream; b, Tim's Creek; (x ± 1 SE, n = 5). Error bars associated with some data points are encompassed by the symbol.

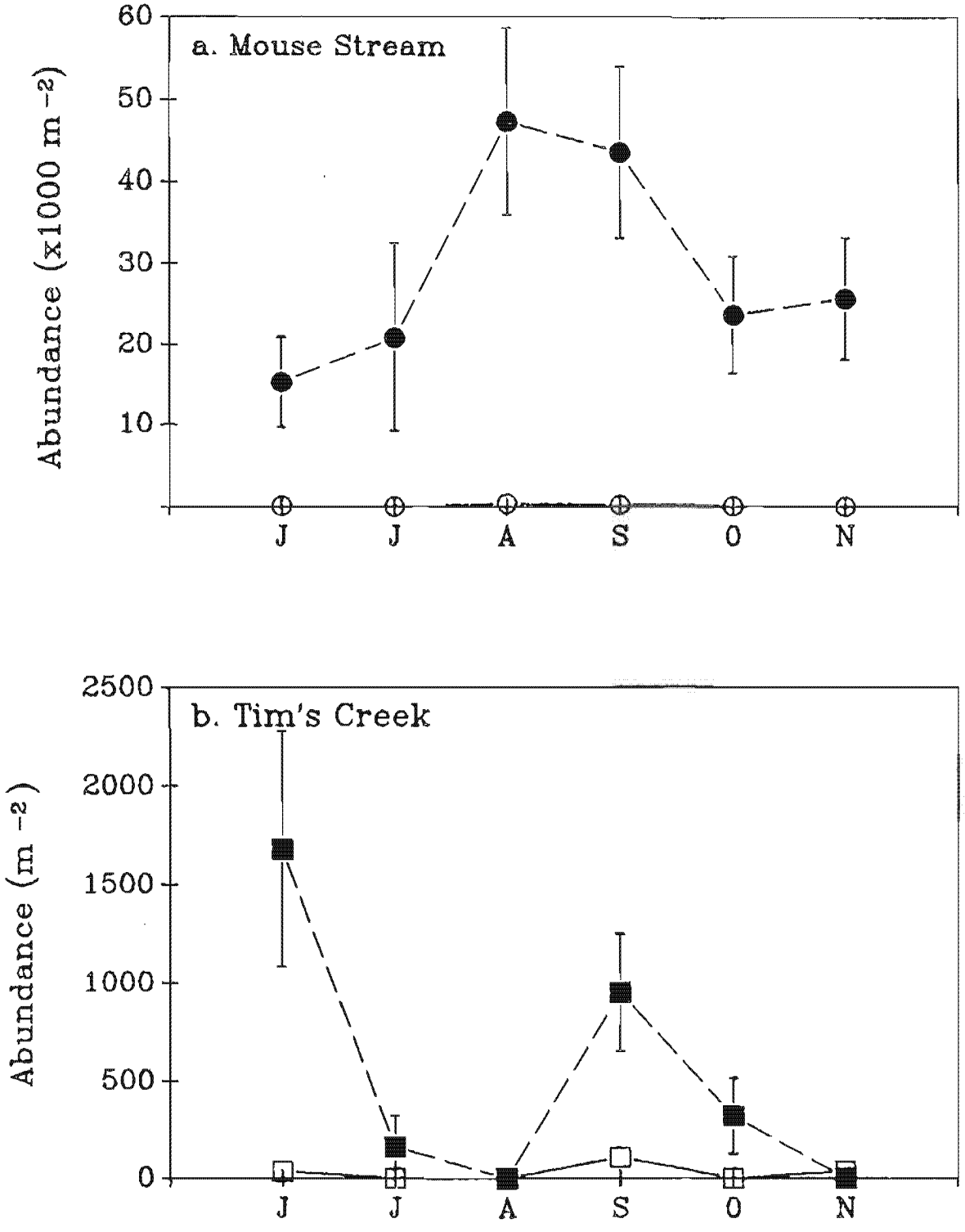


Fig. 8: Abundance of Tardigrada associated with bryophytes (closed symbols) and riffles (open symbols) at a, Mouse Stream; b, Tim's Creek (x ± 1 SE, n = 5). Error bars associated with some data points are encompassed by the symbol.

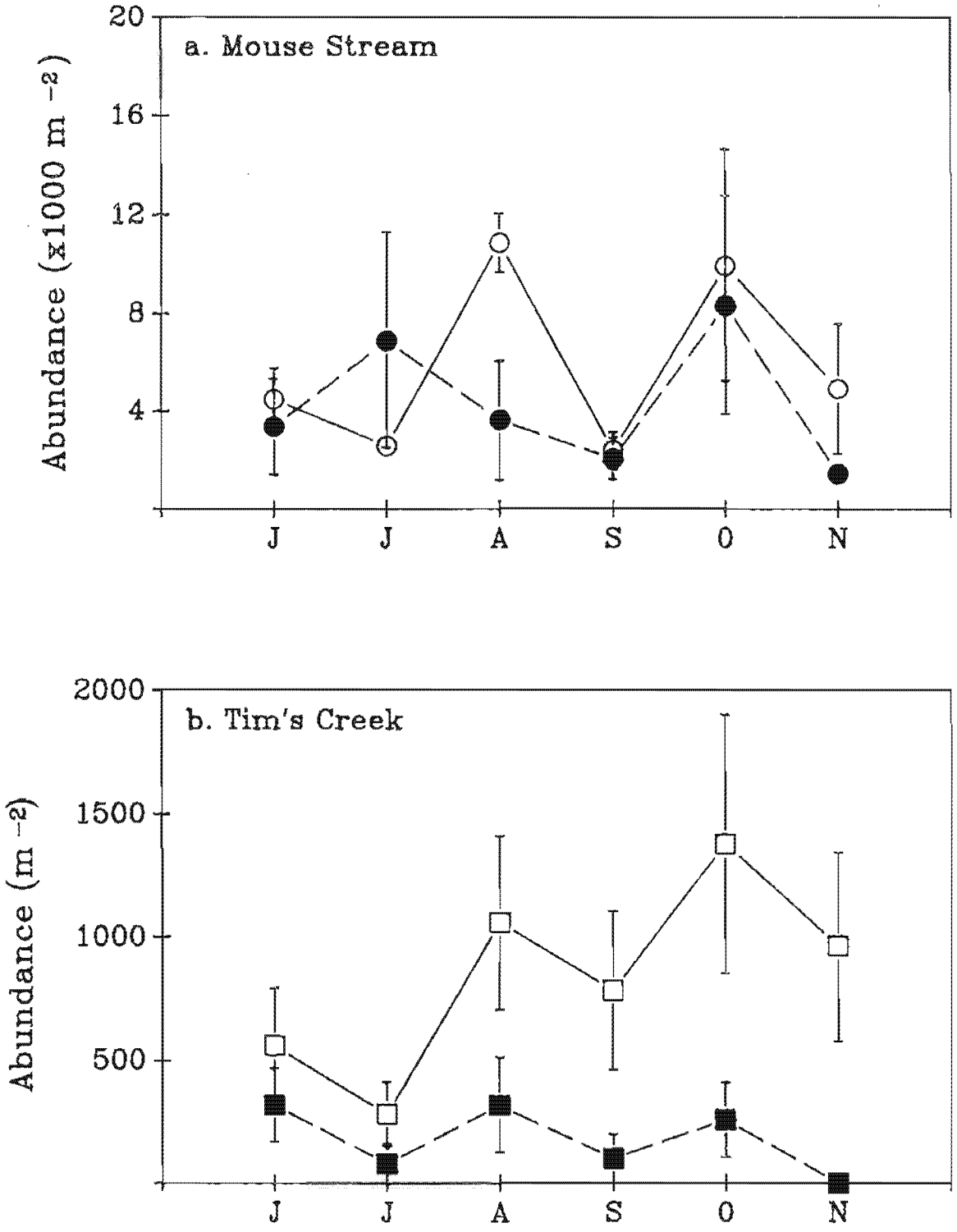


Fig. 9: Abundance of Ostracoda associated with bryophytes (closed symbols) and riffles (open symbols) at a, Mouse Stream; b, Tim's Creek; (x ± 1 SE, n = 5). Error bars from some data points are obscured by the symbol.

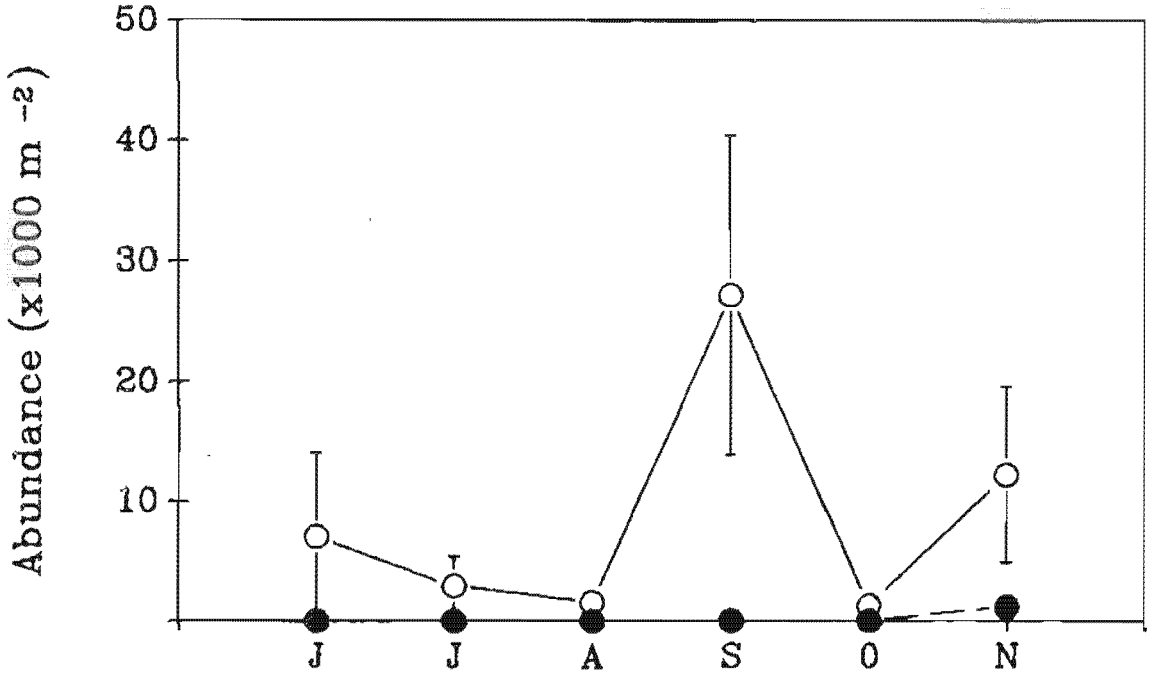


Fig. 10: Abundance of Rotifera associated with bryophytes from Mouse Stream (open symbols) and Tim's Creek (closed symbols); ($x \pm 1$ SE, $n = 5$). Error bars from some data points are obscured by the symbol.

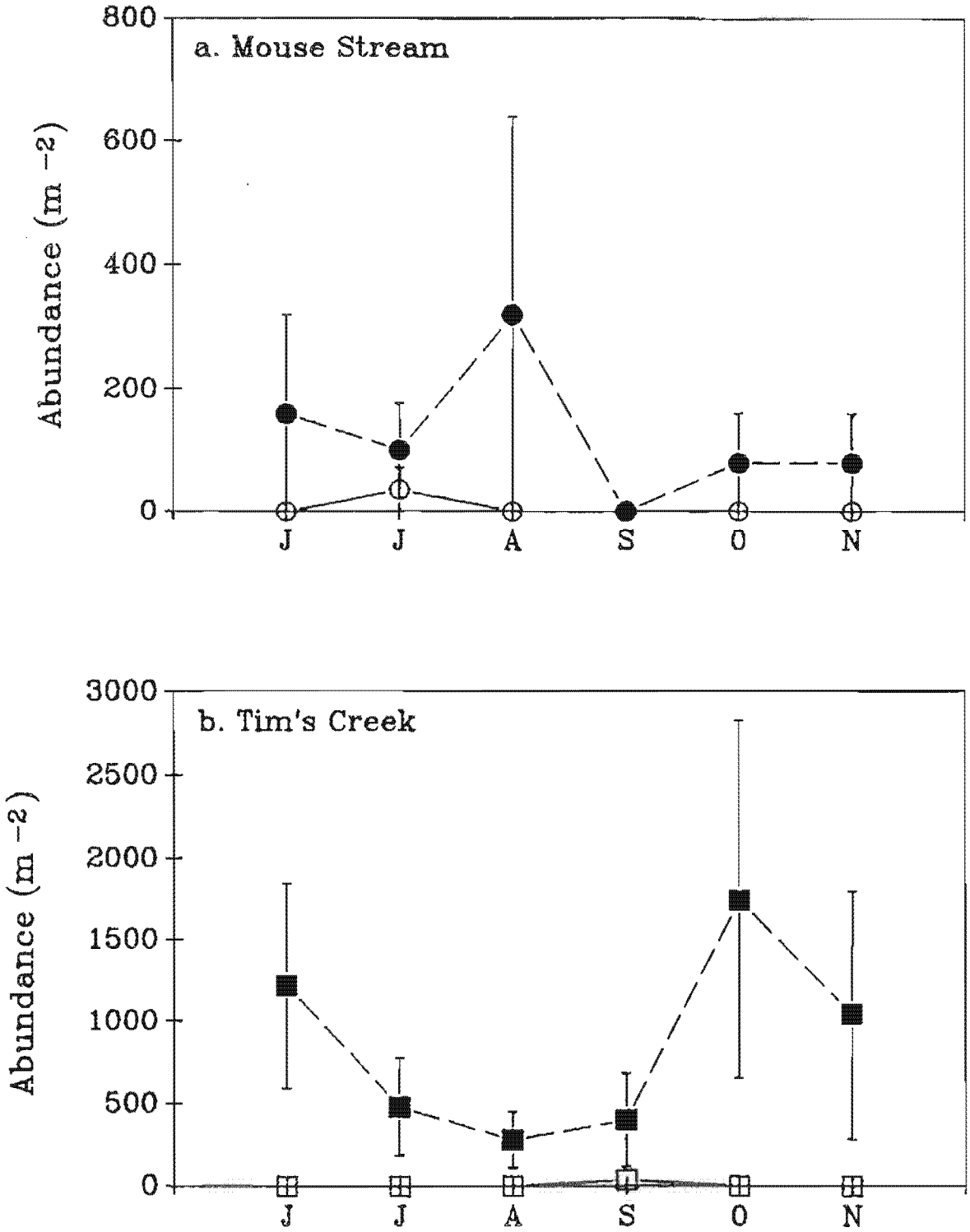


Fig. 11: Abundance of *Anisitsiellides* sp. Associated with bryophytes (filled symbols) and riffle areas (open symbols) at a, Mouse Stream; b, Tim's Creek ($\bar{x} \pm 1$ SE, $n = 5$). Error bars from some data points are obscured by the symbol.

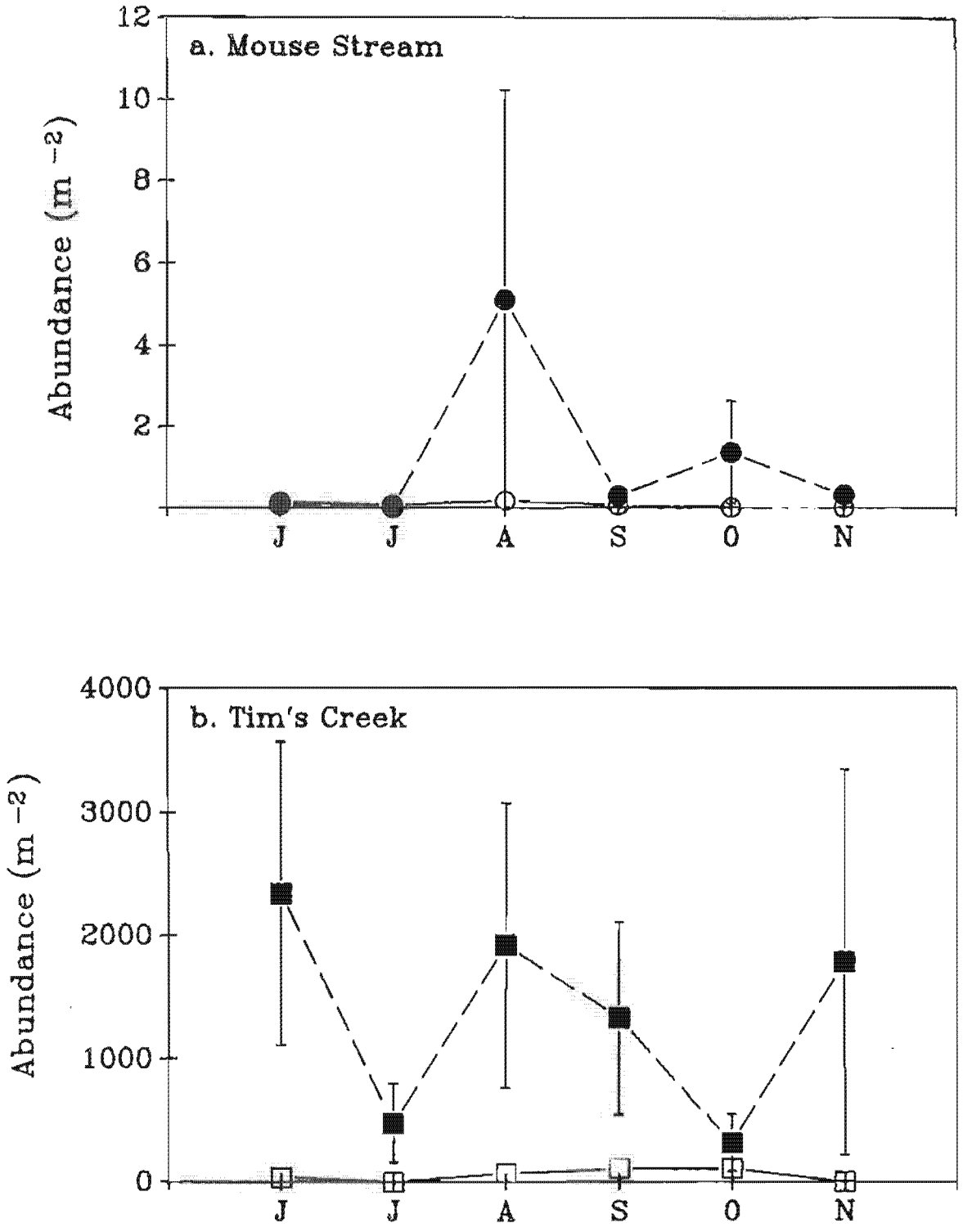


Fig. 12: Abundance of an Oribatid species. A associated with bryophytes (filled symbols) and riffles (open symbols) at a, Mouse Stream; b, Tim's Creek; ($x \pm 1$ SE, n = 5). Error bars from some data points are obscured by the symbol.

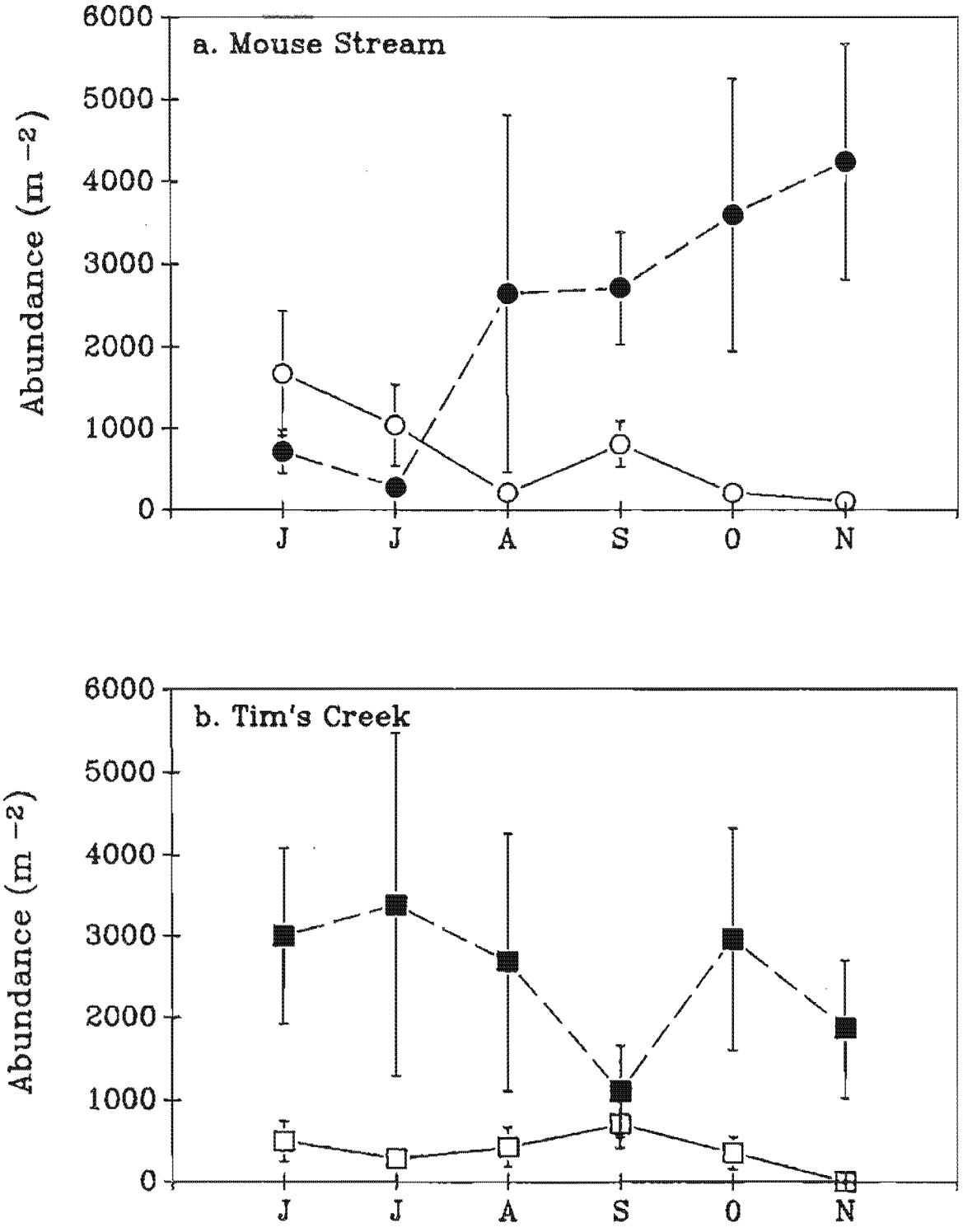


Fig. 13: Abundance of *Paratryssaturus* sp. associated with bryophytes (filled symbols) and riffle areas (open symbols) at a, Mouse Stream; b, Tim's Creek; (x ± 1 SE, n = 5). Error bars from some data points are obscured by the symbol.

Community Ordination

Sample aggregation

Samples from both winter and spring aggregated roughly on DECORANA Axes 1 and 2 into groups corresponding to specific sites or habitats (Fig. 14a,b). Sample aggregations in winter primarily reflected site differences on axis 1 with samples from Tim's Creek having lower scores than samples from Mouse Stream (Fig. 14a). This axis was significantly and negatively correlated with maximum and spot water temperature (reflecting the warmer temperatures of Tim's Creek) and positively correlated with minimum water temperature (Table 2), reflecting the colder waters of Mouse Stream.

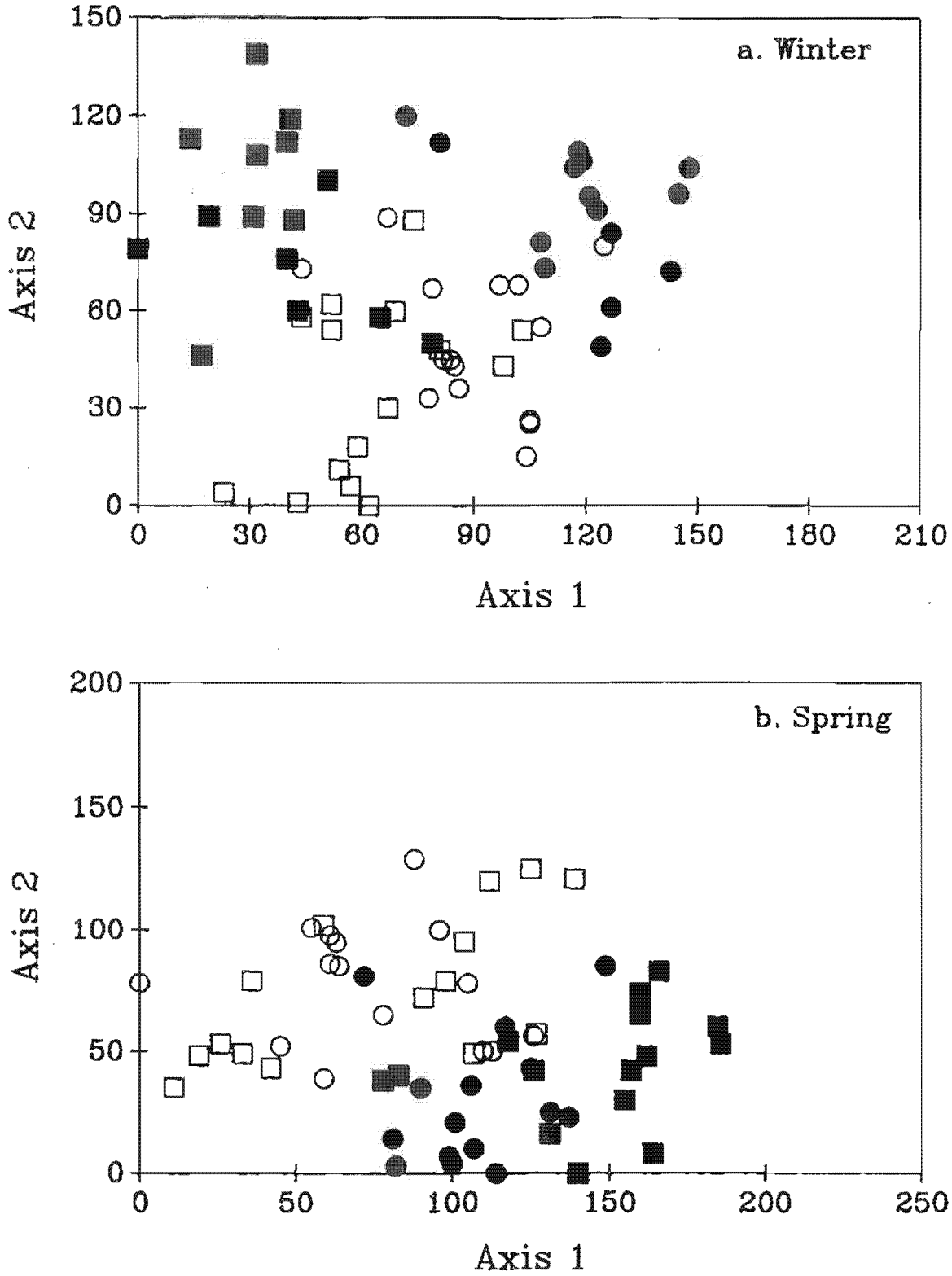
Samples collected from each habitat had distinct distribution patterns along axis 2, whereby bryophyte samples had higher scores than samples from riffles (Fig. 14a). Water depth and velocity were significantly ($p<0.05$) correlated with this axis (negatively and positively, respectively; Table 2), indicating that bryophyte samples were from shallower water and had faster water velocities than riffle samples.

Sample aggregations were less clear in spring because of changes in species composition and density at each site, although samples collected from bryophytes at Tim's Creek had higher axis 1 scores. These were significantly ($p<0.05$) and positively correlated with organic matter and water velocity (Table 2), indicating that organic matter biomass here was high despite the faster waters. Samples collected from bryophytes at Mouse Stream were characterised by low axis 2 scores. These were significantly and negatively correlated with water velocity and minimum water temperature (Table 2), reflecting the cold, fast waters flowing over the plants at this site.

Site and habitat differences in assemblage composition

Abundances of nine meiofaunal groups were significantly correlated with sample scores on DECORANA axes 1 and 2, corresponding to samples from Mouse Stream. Tardigrades, copepods and ostracods showed such correlations three times indicating strong associations of these taxa with this site. In contrast, 13 OTUs were significantly correlated with samples from Tim's Creek. Most of these were aquatic mites, with *Anisitsiellides* sp.B and *Zelandobatella nalas* Hopkins (Hygrobatidae) showing such correlations on 3 occasions (Table 3). Thus, microcrustaceans appeared to be diagnostic of samples collected from Mouse Stream, whereas aquatic mites were restricted more to Tim's Creek.

Abundances of 12 OTUs were significantly correlated with bryophyte samples, most on more than one occasion (Table 3) indicating strong associations with this habitat. In contrast, only 7 OTUs were significantly correlated with riffles (Table 3), and these taxa displayed such correlations only once or twice. Thus more meiofaunal taxa were consistently found within bryophytes than riffles, presumably reflecting the more benign habitat of the former.



Figs 14a,b: DECORANA plots of samples from bryophyte and riffle habitats at Mouse Stream and Tim's Creek in a, winter; and b, spring. Samples from Mouse Stream are denoted by open circles (riffles) and closed circles (bryophytes) whereas samples from Tim's Creek are denoted by open squares (riffles) and closed squares (bryophytes).

Table 2: Significant ($p < 0.05$) Pearson correlation coefficients (r) between sample scores on DECORANA axes 1 and 2 and selected environmental variables taken from each habitat during the study. At the top of each column is a description of the sample clusters on each axis, showing if they aggregated with low axis scores (-ve) or high axis scores (+ve); MS = Mouse Stream; TC = Tim's Creek.

Variable	AXIS 1				AXIS 2			
	Winter		Spring		Winter		Spring	
	TC (-ve)	MS (+ ve)	Other Samples (-ve)	TC moss (+ve)	riffles (-ve)	moss (+ve)	MS moss (-ve)	Other samples (+ve)
LPOM				0.359				
CPOM				0.409				
MPOM				0.320				
Temperature								
maximum	-0.692							
minimum		0.203					-0.383	
spot	-0.450							
water depth			-0.584		-0.500			0.354
current velocity				0.441		0.589	-0.458	

Table 3: OTUs whose abundances were significantly ($p < 0.05$) correlated with the location of samples plotted on DECORANA axes 1 and 2. Sample aggregates on each axis could be distinguished on the basis of site or habitat differences, with aggregates from specific sites or habitats having lower or higher axis scores than others. Abundances of individual meiofaunal taxa were correlated with the sample scores on each axis to determine if invertebrate abundances were correlated with these scores, and by inference to particular sites or habitats. The number of times each OTU displayed such correlations is given under the specific site or habitat location.

	SITE		HABITAT	
Operational Taxonomic Unit (OTU)	Mouse Stream	Tim's Creek	Bryophytes	Riffles
Chironomidae	2	1	1	
Tardigrada (*Macrobiotis dispar*)	3	1	3	
Nematoda	1	1	2	
Copepoda	3	1	3	
Ostracoda	3	1		2
Rotifera	2		2	
Anisitsiellides sp. B		3	2	
Oribatida sp. B	1	2	3	
Euwandesia sp.		1		2
Unidentified Acarina larvae		1		1
Zelandobatella naias		3	3	2
Oribatida sp. A	1	2	2	
Paratryssaturus sp.		2	2	2
Pseudotryssaturus acutus			1	1
Neomomonia sp.	2	1	1	1
Total number of OTUs	9	13	12	7

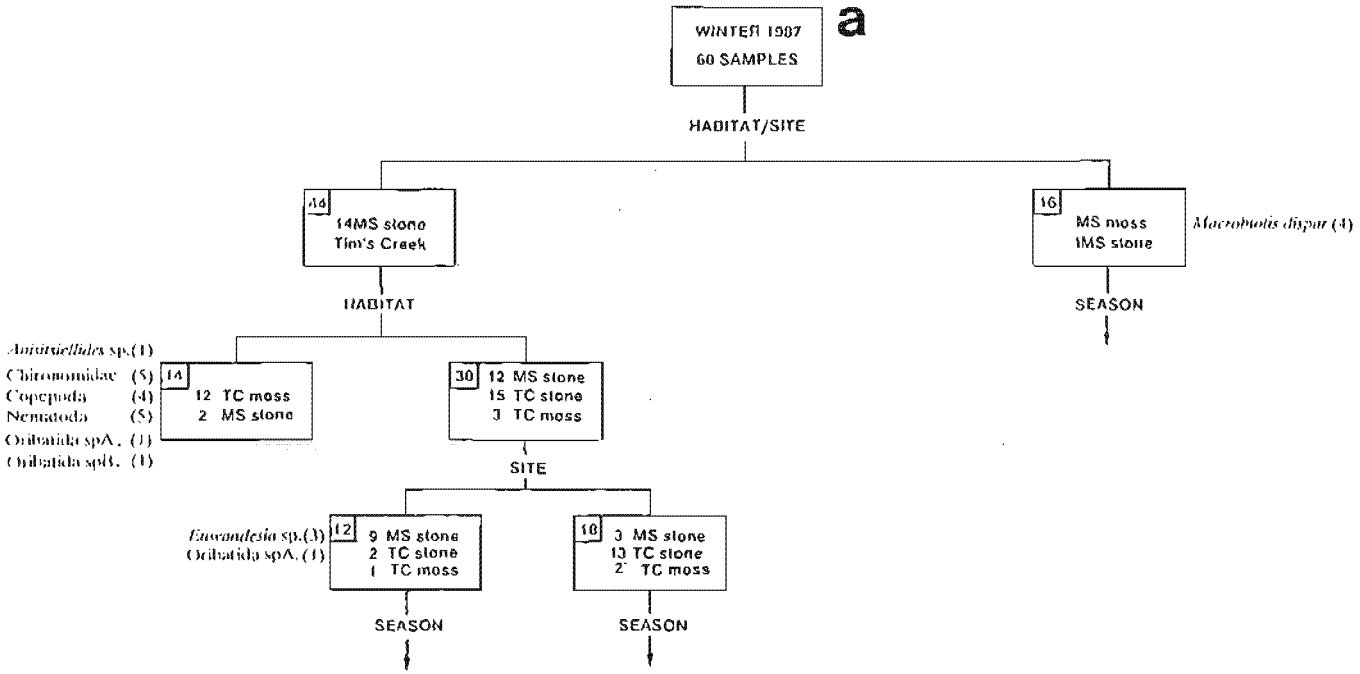
Community classification

Classification of samples by TWINSPAN indicated that bryophytes and riffles contained distinct meiofaunal assemblages (Fig 15 a,b). TWINSPAN divisions were based initially on habitat dichotomies, and most bryophyte samples grouped together in both seasons. Divisions of riffle habitats however, were greatly affected by seasonal variations in taxonomic composition and abundance, which obscured any differences between the meiofaunas of each site. This reflects the more consistent associations of meiofaunal taxa within bryophytes than riffles (as observed in the DECORANA analysis) whereby presence of taxa within riffles was more transitory and consequently affected the TWINSPAN analysis.

Pseudospecies analysis

Six pseudospecies were identified by TWINSPAN as indicators for Mouse Stream, 4 representing high invertebrate densities (Table 4). In contrast, only 2 pseudospecies were diagnostic of Tim's Creek, and both represented low invertebrate densities. This highlights the common occurrence of taxa with high densities at Mouse Stream, the paucity of those taxa commonly found at Tim's Creek, and low abundances of those that were. Twelve pseudospecies, including 8 high density "taxa" were indicative of bryophyte samples (Table 4), reflecting the high densities of invertebrates commonly associated with bryophytes. No pseudospecies, however, were indicative of riffles. This supports the DECORANA analysis which illustrated that riffle dwelling taxa were mainly low density, transitory species, none of which was present commonly enough to be a pseudospecies indicator of riffles.

Figs 15a,b: TWINSPAN classifications of samples collected monthly from bryophytes and riffles in Mouse Stream and Tim's Creek. Dendrograms show sample groupings produced at each TWINSPAN division, the number of samples in each grouping (small box) and a description of these samples (larger box). At each division, the primary basis for sample separation (site, habitat, or a combination of both) is shown. Indicator pseudospecies characteristic of samples within each sample group are given, the number in parentheses being the pseudospecies abundance score. Divisions were terminated when samples within a group differed only by season. Two TWINSPAN analyses were conducted in a, winter and b, spring.


a
WINTER 1987
60 SAMPLES
HABITAT/SITE
44
14MS stone
Tim's Creek
16
MS moss
1MS stone
Macrobiotis dispar (4)
HABITAT
SEASON
Anisitsiellides sp.(1)
Chironomidae (5)
Copepoda (4)
Nematoda (5)
Oribatida spA. (1)
Oribatida spB. (1)
14
12 TC moss
2 MS stone
30
12 MS stone
15 TC stone
3 TC moss
SITE
Enwondesia sp.(3)
Oribatida spA.(1)
12
9 MS stone
2 TC stone
1 TC moss
18
3 MS stone
13 TC stone
2 TC moss
SEASON
SEASON

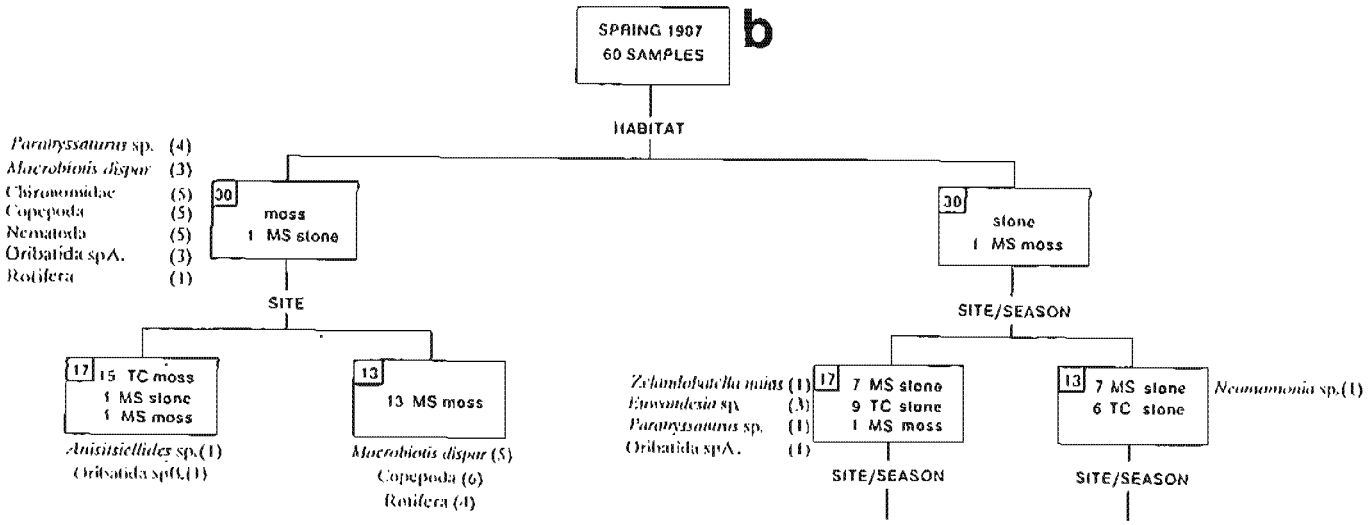

b
SPRING 1987
60 SAMPLES
HABITAT
Paramyssaurus sp. (4)
Macrobiotis dispar (3)
Chironomidae (5)
Copepoda (5)
Nematoda (5)
Oribatida spA. (3)
Rotifera (1)
30
moss
1 MS stone
30
stone
1 MS moss
SITE
SITE/SEASON
17
15 TC moss
1 MS stone
1 MS moss
13
13 MS moss
Zchamlofaiella minis (1)
Enwondesia sp\ (3)
Paramyssaurus sp. (1)
Oribatida spA. (1)
17
7 MS stone
9 TC stone
1 MS moss
13
7 MS stone
6 TC stone
Neomamonia sp.(1)
Anisitsiellides sp.(1)
Oribatida spB.(1)
Macrobiotis dispar (5)
Copepoda (6)
Rotifera (4)
SITE/SEASON
SITE/SEASON

Table 4: Indicator species (represented here by pseudospecies) as determined from TWINSPAN analysis of the seasonal meiofaunal data. At each level in the TWINSPAN classification, samples were placed into smaller subgroups based on similarity in species composition. Pseudospecies represent abundance classes of each taxon (see text), and are defined by name and abundance class (parentheses).

SITE		HABITAT	
Mouse Stream	Tim's Creek	Bryophytes	Riffles
		Chironomidae (5)	
Tardigrada (5)		Tardigrada (4)	
Tardigrada (4)		Tardigrada (3)	
		Nematoda (5)	
Copepoda (6)		Copepoda (5)	
		Copepoda (4)	
Rotifera (4)		Rotifera (1)	
Euwandesia sp. (1)			
	Oribatida sp. B (1)	Oribatida sp. B (1)	
Oribatida sp. A (1)		Oribatida sp. A (1)	
		Paratryssaturus sp. (4)	
	Anisitsiellides sp. B (1)	*Anisitsiellides* sp. B (1)	
Number of pseudospecies 6	2	11	0

DISCUSSION

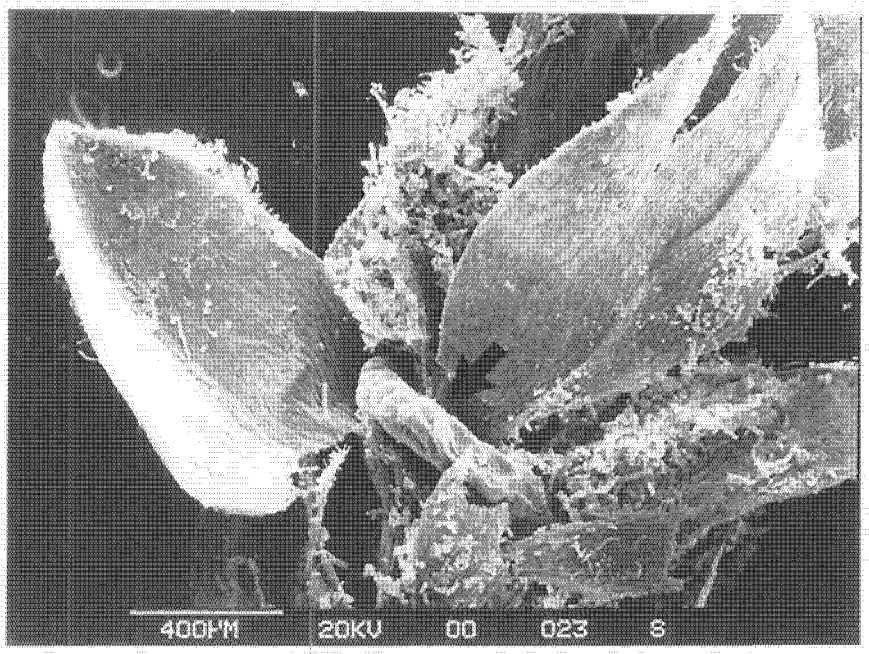
It has been postulated that invertebrates colonize bryophytes in response to either the shelter they provide, or their associated and often abundant detrital and algal food (Glime & Clemons 1972, McKenzie-Smith 1987, Smith-Cuffney 1987, Cox 1988). I found that bryophytes trapped more detritus (i.e., FPOM and UFPOM) than riffles, thereby transforming essentially erosional habitats into depositional zones of high habitat stability. Although microcrustaceans are often associated with silt-laden environments (Shiozawa 1986), I found no significant correlations between meiofauna abundances and quantities of fine organic matter as expected. Instead, the distribution of meiofaunal taxa may have been more strongly associated with periphyton upon which many of these are known to feed (e.g., Spaul 1973, Chapman & Lewis 1976, Jennings 1976, 1979, Davis 1981).

The only correlations observed between organic matter biomass and meiofaunal abundance were the positive correlations between LPOM, CPOM, and MPOM and sample aggregates associated with Tim's Creek bryophytes on axis 1 in spring. While this is unlikely to imply a direct feeding relationship of meiofauna on bryophytes, it may imply utilization of bryophytes and associated detritus as shelter from the high water velocities at this site during spring.

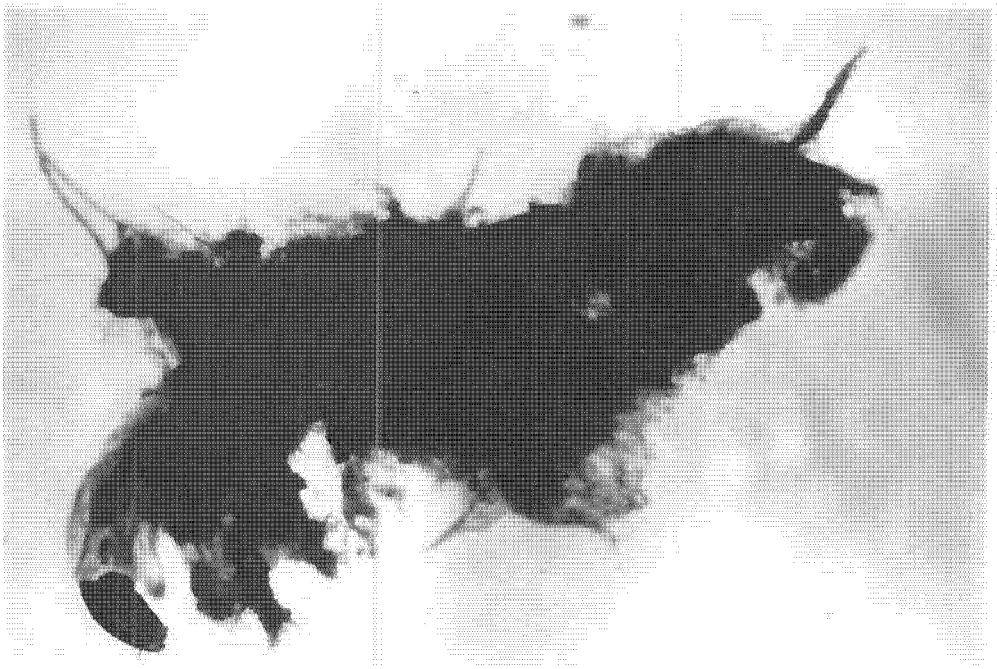
Furthermore, the observation that the cyclopoid copepods *Bryocamptus vejdovskyi* Mrazek and *B. zschokkei* Schmeil can be found in the hyporheos in erosional habitats (Shiozawa 1986) suggests that the meiofauna often seeks refuge from the fast currents above them by burrowing into the hyporheos (Williams & Hynes 1974, Williams 1989). This behaviour reflects the inability of meiofaunal taxa to tolerate high current velocities (Winner 1975, Chapman & Lewis 1976). Thus, meiofaunal taxa associated with bryophytes may be utilising these plants as a "biotic hyporheic region", whereby instead of dwelling between the interstices of inorganic substrata, they dwell amongst bryophyte stems and associated trapped detritus and periphytic algae.

The importance of bryophytes as a physical substratum for meiofaunal invertebrates is clear from my observations of small chironomids and tardigrades that dwell amongst leaf axils of many plants (Figs 16,17,18). Several taxa (e.g., chironomids, nematodes, copepods and tardigrades) seem to move around the adaxial leaf surface and crawl up the stem close to leaf insertions. Numerous chironomid larvae were also observed to burrow into stem apices (Fig. 19), where some large individuals construct "pupation chambers" (Fig. 20). Nematodes were found amongst trapped detritus and algae on the plants.

Figs **16a,b**: Scanning electron micrograph of an early instar chironomid larva (arrowed) half exposed as it moves along a stem of *Bryum blandum* collected from Mouse Stream (a). Many larvae were observed burrowing into detritus and algae that were often intimately associated with bryophytes (b).



a



b

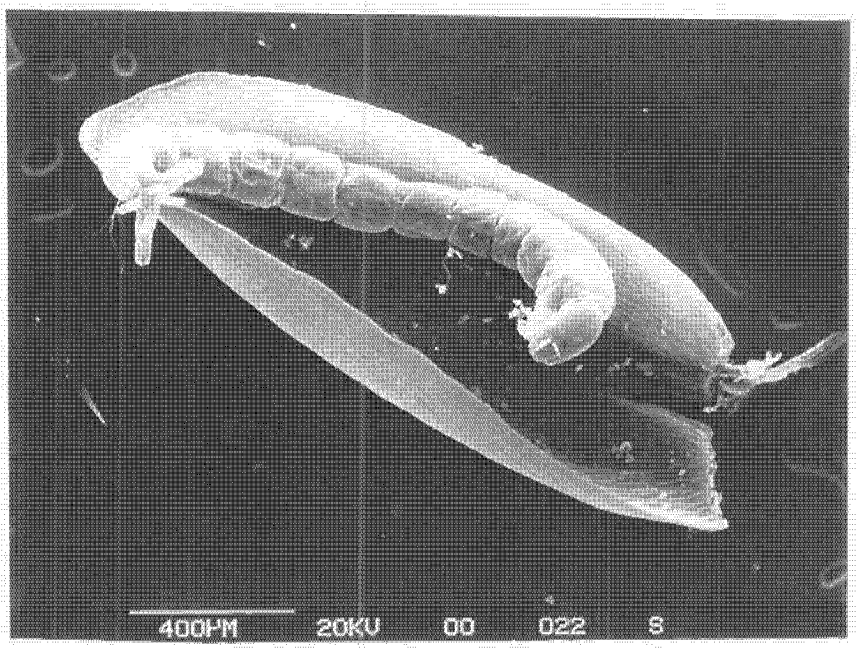


Fig. 17: Scanning electron micrograph of a small chironomid larvae nestled into the concave leaf of *Bryum blandum* where it would have escaped the often strong water currents flowing above the plant. Many chironomid larvae and other small invertebrates were seen dwelling within the adaxial region of moss leaves between the leaf and the stem.

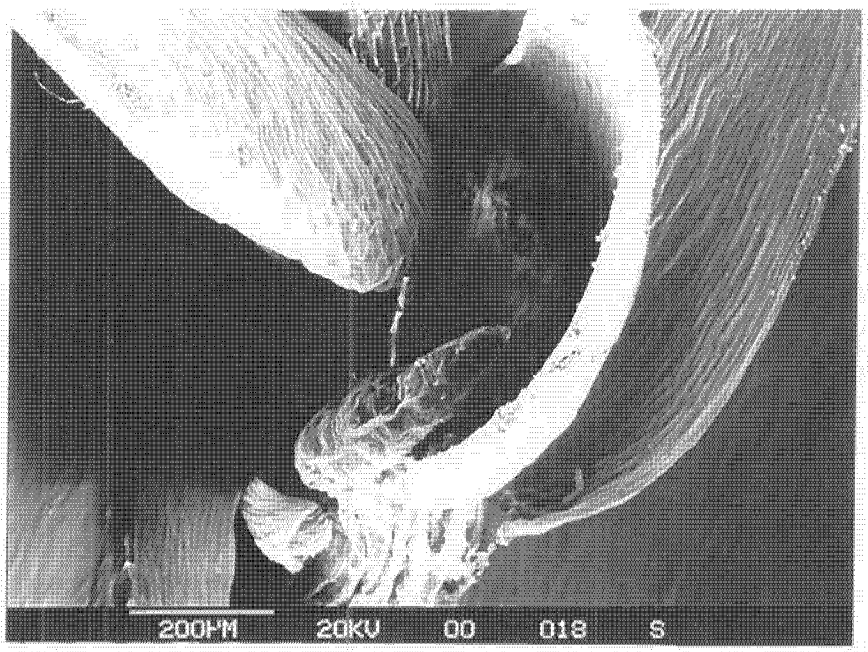


Fig. 18: Tardigrades were often observed crawling along stems, and within leaf axils of bryophytes. The scanning electron micrograph shows *Macrobiotis dispar* as it travels up a stem of *Bryum blandum*, keeping between the concave leaf and the stem.

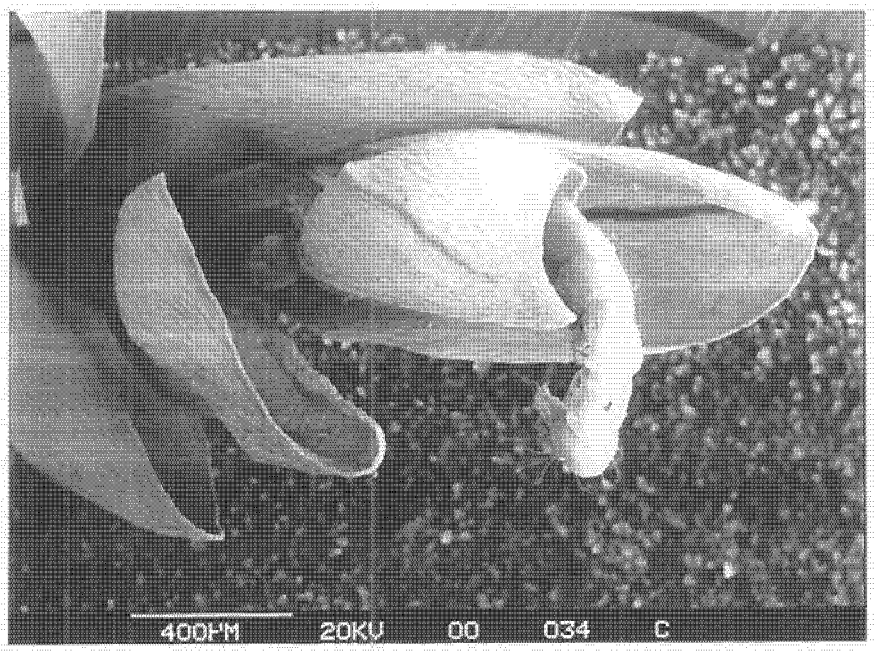


Fig. 19: Scanning electron micrograph of a chironomid larva burrowing into the apex of a *Bryum blandum* stem. These animals were commonly seen to behave in this way, either in search of food, shelter or a place to pupate.

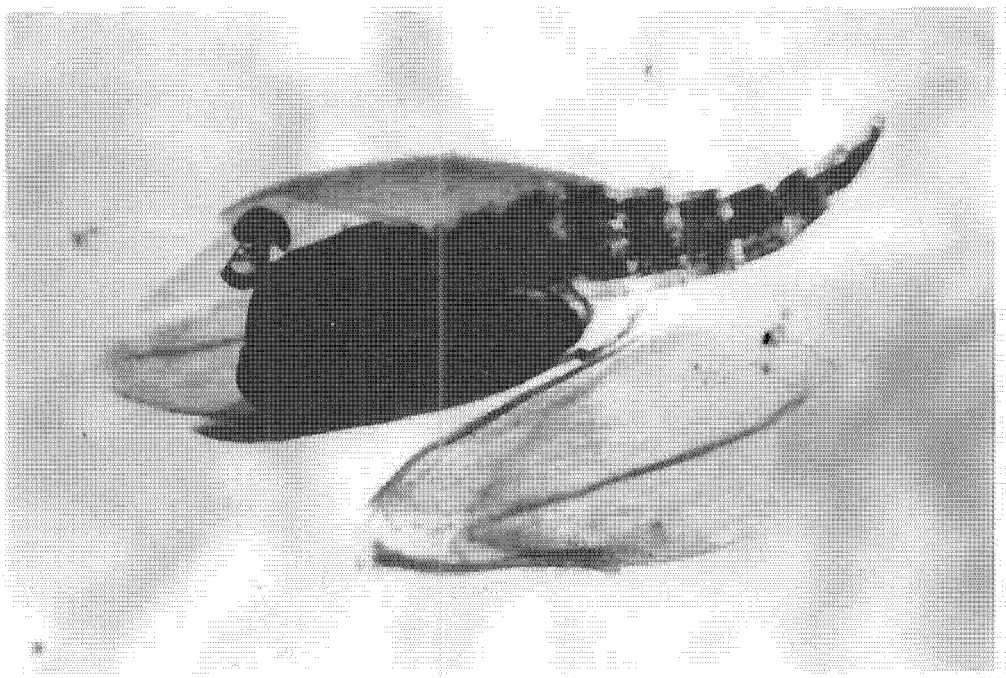


Fig. 20: Chironomids often constructed "pupation chambers" from stem apices of various mosses. There, a chironomid larva is pupating within the stem apex of *Bryum blandum*.

The two sites were characterised by different temperature regimes whereby Mouse Stream was usually colder. Water temperature variables were correlated with sample aggregations corresponding to discrete site groupings, as shown by DECORANA. Although the harpactacoids *Atheyella crassa* Sars, *Bryocamptus zschokkei* and *B. echinatus* Mrazek tend to be restricted to warmer waters (Rundle & Hildrew 1990) and development times for harpactacoids decrease with increasing temperature (Sarvala 1979, O'Doherty 1985), I found that harpactacoids were more abundant at the colder site. This is likely to reflect the greater periphyton biomass, and therefore food at the open site (Chapman & Lewis 1976).

The greater abundance of aquatic mites at Tim's Creek may reflect the warmer waters there, however, and hydrachnellid mites like harpactacoids were found to be more prevalent in warmer waters (Rundle & Hildrew 1990). Many water mites are parasitic on aquatic insects as larvae (Smith 1988) and numerous *Zelandoperla* larvae at Tim's Creek were observed to be heavily infested with these animals. Thus, the higher densities and diversity of mites at this site may also reflect increased availability of potential hosts, a factor implicated as being responsible for enhanced densities of hydrachnellid mites in circumneutral sites in rifles in streams of the Ashdown Forest, Southern England (Rundle & Hildrew 1990).

The meiofauna encountered at both Arthur's Pass sites was dominated by chironomids (46%), nematodes (18%) and copepods (17%), with tardigrades, ostracods, rotifers and mites contributing only a small proportion to the assemblage. Chironomids also dominated hyporheic meiofaunal assemblages taken from two small rivers in southern Ontario, Canada, whereas harpactacoid copepods were only minor constituents of the stream fauna at these sites (Williams 1989).

Although previous investigations of invertebrates associated with bryophytes (e.g., Percival & Whitehead 1929, Hynes 1961, Glime 1968b, Stern & Stern 1969, Cowie & Winterbourn 1979, Brusven *et al.* 1990) were all conducted by sampling with a larger mesh size, and only reported on the macrofauna (i.e. animals collected on a sieve of 250 µm or larger), it is likely that the numerical dominance of chironomids reported in these studies reflects a high abundance of these animals in smaller (unsampled) size classes.

The chironomid larvae observed at high densities in my study were primarily species of Orthocladiinae, a subfamily frequently associated with bryophytes (Welch 1976, Cranston 1982). The large numbers of first instar individuals found suggests that oviposition occurs there and the abundance of larvae of all sizes indicates that bryophytes provide abundant food and shelter.

In contrast to my findings, Cox (1988) found that the meiofauna associated with both *Fontinalis novae-angliae* Sull. and *Eurhynchium riparioides* (Hedw.) Rich. in two second-order streams in Tennessee, U.S.A. was dominated by rotifers (up to 94% of total invertebrate density), a group that comprised < 2.0% of the invertebrates associated with bryophytes at Mouse Stream. This is unlikely to be a consequence of

sampling methodology, but rather reflects an actual paucity of these animals in the two alpine streams studied.

Meiofaunal densities in bryophyte samples from the two streams were less than those reported for various meiofaunal groups occurring on terrestrial moss at Signy Island, Antarctica (e.g., Spaul 1973, nematodes; Jennings 1979, tardigrades; Maslen 1981, nematodes). However, mean nematode density among bryophytes at Mouse Stream (1.85×10^5) was similar to values reported by Zullini & Ricci (1980) for a small Italian stream, and by Cox (1988) for a small forested American stream (1.0×10^5 m^{-2} and 1.69×10^5 m^{-2}, respectively). Similarly, tardigrade densities in my study (2.8×10^4 individuals m^{-2}) were comparable to those found by Cox (1988) (9.86×10^4), although crustaceans (copepods and ostracods) were more abundant in my samples than his (1.64×10^5 m^{-2}, compared to 2.76×10^4 m^{-2}). This may reflect the higher biomass of periphyton on bryophytes in my study, as periphyton did not appear as abundant on his plants as it did on the plants in my study.

In most cases, densities of meiofaunal taxa per unit area of stream bed were higher at Mouse Stream than Tim's Creek, and within bryophytes than riffles. Each stream was characterised by frequent storm flows and sometimes extensive substrate instability, and currents immediately above bryophyte mats were always faster than those above stony substrata. Current velocities around bryophyte stems, and those within the matrices of plants would have been considerably less at all times, however, and as Devantry (1987) has pointed out, such buffered conditions provide high habitat stability. Thus, taxa associated with bryophytes should experience both slower currents and greater environmental constancy than those present amongst riffle substrata, and this may explain their high abundances.

Also associated with bryophytes at each site were large quantities of periphyton (especially at Mouse Stream) and trapped detritus (especially at Tim's Creek). The presence of such an abundant potential food source must also attract invertebrates to this habitat. Free-living nematodes are known to be primarily microbial feeders, consuming either algae, bacteria or fungi (Spaul 1973, Sohlenius 1979, 1980, Maslen 1981, Davis 1981) and some tardigrades feed on algae and mosses by puncturing cell walls with their stylets (Higgins 1959, Jennings 1976, 1979, Davis 1981). Chironomids in bryophyte samples taken from both sites were observed to move along plant stems, grazing periphyton and trapped detritus. Copepods are also known to "graze" upon periphyton and trapped microbial "Aufwuchs" that occurs on bryophyte stems (Chapman & Lewis 1976).

Investigations of meiofaunal abundance in mosses at Signy Island (Caldwell 1981, Maslen 1981) have shown that invertebrate density is highest in the top few centimetres of the mat. This corresponds with the zone of highest algal density (Broady 1979) and suggests that algae are important foods for many of these animals. This may help explain the very high invertebrate densities within bryophyte mats at Mouse Stream, and within bryophytes (see Chapter 7).

Finally, investigations into lentic and marine meiofauna have established their often significant role in community metabolism (e.g., Anderson & de Henau 1980, Sarvala 1986, Strayer & Likens 1986, (lentic studies); Gerlach 1971, 1978 (marine studies). Although the lotic meiofauna have been considered in a few studies, both high densities (e.g., Williams & Hynes 1974, Zullini 1976, Shiozawa 1986) and high production values reported (O'Doherty 1985) imply that this group can make a significant contribution to energy dynamics in streams. Most investigations of lotic meiofauna have sampled second order (or greater) streams (Williams & Hynes 1974, O'Doherty 1985, Williams 1989) and although Valley Creek (U.S.A.) examined by Shiozawa (1986) and 8 of the 30 English streams examined by Rundle & Hildrew (1990) were first order tributaries, they were considerably larger than either of my study streams. In fact, Mouse Stream was a very small, spring fed, headwater stream less than 50 m long, yet it supported extremely high densities of meiofauna. In order to maintain such a high density, individuals must avoid being washed downstream, something they do by colonizing bryophytes.

Unlike most insect taxa that leave the stream environment upon emergence, most aquatic meiofaunal taxa have no terrestrial stages, and consequently most carbon assimilated by these animals and not respired will remain in the stream. Secondary production of the harpactacoid copepod *Bryocamptus zschokkei* (396 mg m^{-2} y^{-1}, O'Doherty 1985) in a second order North Carolina (U.S.A.) stream was calculated to be not much less than that of a dominant shredding plecoptera, *Peltoperla maria* (500 mg m^{-2} y^{-1}, O'Hop *et al.* 1984). This, coupled with the fact that copepod biomass produced as eggs is often very high (O'Doherty 1985) indicates that meiofaunal taxa can contribute significantly to stream metabolism. Despite their small size, the abundant meiofauna associated with bryophytes in Mouse Stream and Tim's Creek are likely to play an important, if yet unknown, role in the energy transfer within each system.

CONCLUSIONS

It is clear that high densities of meiofauna, notably species of Tardigrada, Nematoda, Copepoda, Rotifera and Chironomidae have intimate associations with bryophytes. These taxa occur in vastly higher numbers within bryophytes than in riffles. Different meiofaunal communities were found associated with aquatic bryophytes in the two streams above the tree-line compared with below, and may reflect the higher quantities of algae colonizing bryophytes above the tree-line.

As in previous investigations of the hyporheos of streams, the meiofauna encountered within bryophytes is postulated to utilise these plants primarily as an escape from erosional currents. While hyporheic taxa burrow between interstices of mineral substratum particles, meiofauna associated with bryophytes burrow and also dwell along stems and in leaf axils of these plants where they seek shelter.

Very few studies have examined lotic meiofauna, and this study represents the first in New Zealand alpine streams. In total, I recorded 22 OTUs, of which at least 6 are undescribed (2 Copepoda and 4 Acarina). Because the meiofauna associated with bryophytes achieved very high densities, they may play an important role in energy transfer.

CHAPTER FOUR:

ASSESSMENT OF ARTIFICIAL BRYOPHYTES FOR

INVERTEBRATE SAMPLING

INTRODUCTION

Bryophytes play a number of important roles in the lotic environment. These include primary production, reduction of water flow, filtration and retention of water-borne detritus and the provision of a food source and habitat for aquatic organisms. Rheophilous bryophytes grow only on stable bedrock (Heywood 1362) and are generally restricted to turbulent, low-order, headwater streams (Glime 1970, Naiman 1983, Sheath *et al.* 1986) because of their inability to utilise dissolved bicarbonate ions and dependence on atmospheric CO_2 for photosynthesis (Bain & Proctor 1980, Allen & Spence 1981).

In these normally erosional habitats, bryophytes greatly reduce current velocities within their matrices and abate extremes of water movement (Devantry 1987). A consequence of this is that abundant periphyton and large quantities of detritus are often associated with bryophytes (Johnson 1978, Maurer & Brusven 1983, Smith-Cuffney 1987). The presence of these materials can result in enhancement of invertebrate densities far beyond that which can be explained simply by an increase in colonisable surface area provided by the bryophytes themselves (McKenzie-Smith 1987). Numerous studies have also shown that aquatic bryophytes support higher densities of invertebrates than adjacent riffles (e.g., Carpenter 1927, Percival & Whitehead 1929, 1930, McElhone & Davies 1983, Brusven *et al.* 1990) and suggest that the invertebrates are responding to the presence of trapped detritus and periphyton amongst these plants.

Invertebrates living on and among bryophytes rarely feed on this plant material directly (Gerson 1972, Lawrey 1987) although there are some reports of aquatic bryophyte herbivory (e.g., Alexander 1920, Byers 1961, Mutch & Prichard 1984a, b, Gerson 1985, Willoughby & Mappin 1988). The value of bryophytes to invertebrates may therefore be associated primarily with their "non-trophic" properties, and in a number of studies, artificial bryophytes have been found to support similar assemblages of animals to living bryophytes (Glime & Clemons 1972, McKenzie-Smith 1987). This suggests that colonizers may respond primarily to the physical environment produced by the plants, and associated organic matter.

The objective of the work detailed in this chapter was to describe the construction of artificial bryophyte substrates and to indicate how closely they mimicked natural bryophytes with respect to invertebrate colonization. Their use in detailed experiments on habitat utilization by invertebrates is described in Chapter 5.

MATERIALS AND METHODS

Substrate design

Artificial bryophytes were constructed by weaving pieces of nylon twine (5 cm long, 1 mm thick) into squares (0.01 m^2) of firm nylon mesh (pore size 4 mm). This created a mat-like structure superficially similar to natural bryophytes, the "stems" of which lay over each other when placed in flowing water.

The mesh squares were anchored in place by tying their leading and trailing edges to heavy weights (Fig. 1) that were buried in the substratum to minimise water turbulence. They were placed on clean bedrock from where bryophyte material had been scraped away as part of the regular sampling programme (Chapter 2). Each square was firmly pressed down to assist the development of an essentially laminar flow over the structure.

Field placement and sampling

Two trials were conducted to assess the reliability of the artificial bryophytes in mimicking their real counterparts. Trial 1 was conducted in late spring / early summer of 1986 in a low flow environment in Mouse Stream and Tim's Creek (precipitation 36% less than the long term average). Trial 2 was conducted in autumn 1987 when both study sites experienced high flows (precipitation 34% greater than the long term average).

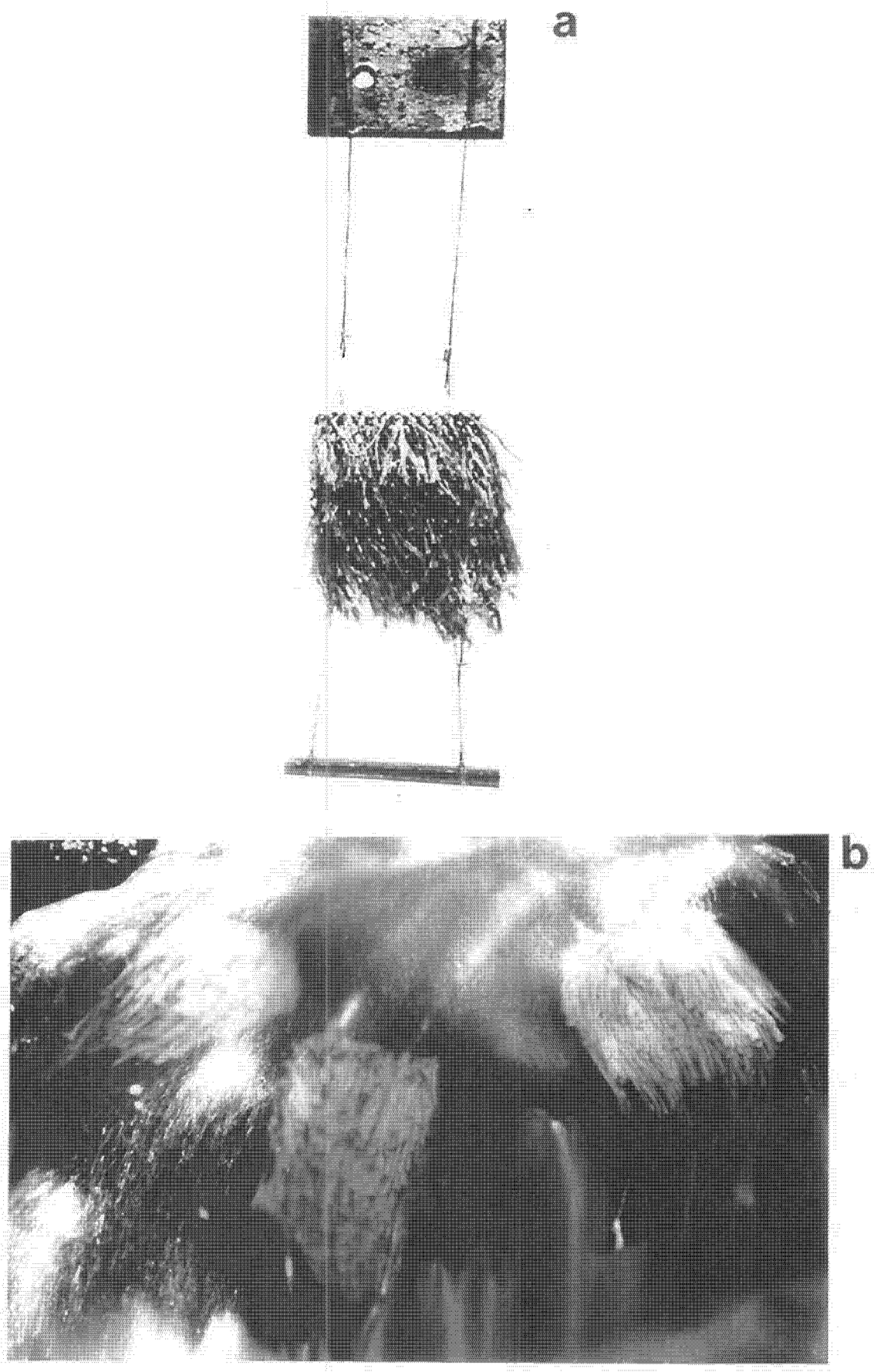


Fig.1: Artificial bryophytes constructed from nylon twine (1 mm thick, 5 cm long) woven into a firm nylon mesh base (10 cm x 10 cm, pore size 4 mm) as shown in a). These were anchored to the substratum by heavy weights tied to the upstream and downstream sides of the structure, which was placed in areas from were all bryophytes had been previously removed. Once in location, mimics were pressed down to ensure a non-turbulent flow over them (e.g., b).

The trials began in October 1986 and February 1987, respectively. For each trial, five replicate artificial bryophytes were placed in a stratified random manner in areas of both streams from which bryophytes had been scrapped away. They were left in place for an 8 week exposure period (as recommended by Lamberti & Resh (1985) for tile substrates).

After 8 weeks, the structures were removed by placing a small Surber sampler (0.022 m^{-2}, mesh size 100 µm) over them and cutting their anchoring strings. The artificial bryophytes were then lifted into the collecting net and material on the underlying bedrock was also washed into the net. Five samples of living bryophytes were obtained by collecting all plant material enclosed by a small Surber sampler (0.01m^2; 100 µm mesh) from bedrock areas with 100% cover. Stony riffles were sampled in a stratified random manner with a larger Surber sampler, which had a foam flange around its base to ensure a proper seal with the substratum (Chapter 2).

Other workers have examined invertebrate communities associated with artificial bryophytes after exposing substrates for various lengths of time. These range from 1 week (Cox 1988) to 4 weeks (McKenzie-Smith 1987; Smith-Cuffney 1987) and even 14 weeks (Glime & Clemons 1972). To determine when invertebrate density, taxonomic richness and algal and detrital biomass reached their maximum levels, I also examined colonization of substrates set out at Mouse Stream for 1, 2, 3, 4, 8, 12, and 16 weeks to determine whether the 8 week exposure time used in the substrate comparisons was optimal.

Sample analysis

Within 6-8 hours of collection, all samples were returned to the laboratory on ice, and frozen (-18°C) pending analysis. Upon thawing, organic material in riffle samples was separated from stones and gravel by elutriation; initial sorting was done by passing each sample through nested sieves (2.0, 1.0, 0.5, 0.25 mm), corresponding to large, coarse, medium and fine particulate organic matter, respectively (LPOM, CPOM, MPOM and FPOM). Bryophytes were teased apart and vigorously stirred and hosed

with high pressure water to dislodge invertebrates before the sample was washed through the nest of sieves. Artificial bryophytes were processed in the same way.

All organic material including animals was collected on sieves and all the material from each sieve was placed in perspex Bogorov sorting trays. Material on the 250 um mesh sieve was decanted into a quadripartite splitter and only one subsample was examined. In a few cases when faunal density was particularly high or the amount of detritus was extremely large, a further subsampling was performed. Invertebrates were identified and counted under a binocular dissecting microscope using diagnostic keys as previously outlined (Chapter 2).

Following removal of invertebrates, all size fractions of organic matter trapped by artificial bryophytes and present in stone and bryophyte samples were dried at 60°C (48 h) and weighed. Ash free dry weight (AFDW) of all organic matter samples was determined after ashing in a muffle furnace (550°C, 12 h).

All substrates in which temporal aspects of invertebrate colonization were investigated were first analysed for chlorophyll *a* content. Samples were thawed and placed in Pyrex evaporating dishes (diameter 12 cm) and covered with 90% ethanol. The containers were sealed with thick PVC plastic film, placed in a water bath (80°C) and left to boil for 10 minutes. After a 2 hour incubation period, 5 ml. subsamples were withdrawn and filtered through Whatman GFC filters (See Appendix 2). Absorbances were measured at 665 and 750 nm (Uvicon spectrophotometer) and following acidification (0.5M HCl, 1 h), absorbances were re-read and pigment values calculated (Sartory and Grobbelaar 1984).

Statistical analyses

My 18 month investigation of invertebrate communities (Chapter 2) had shown that bryophytes support a fauna distinct from that found in riffles. As the study reported in this chapter was carried out to determine if artificial bryophytes supported a fauna more similar to their real counterparts than to riffles, the 10 most common operational taxonomic units (OTUs) found in bryophytes and riffles (Chapter 2), and all OTUs that showed discrete preferences for either habitat (as determined by DECORANA and TWINSPAN; Chapter 2) were analysed (Table 1). Thus I analysed 17 OTUs from bryophyte habitats and 6 OTUs from riffles.

Total invertebrate abundance, taxonomic richness and abundances of these selected taxa were compared by one-way ANOVA following $\log_{10}(x+1)$ transformation using SAS (1985). Where significant differences were observed between habitats, Tukey's Test was used to determine where these differences occurred (Zar 1984, SAS (1988); PROC MEANS).

I was thus able to compare invertebrate densities associated with natural substrates (either bryophytes or riffles) with those from the artificial bryophyte substrates. Three outcomes were possible with such a comparison: that densities were higher on artificial structures than natural; that densities were lower; and that densities were similar (Table 2). On the basis of the ANOVA and Tukey's Test results I was able to objectively assess whether the artificial bryophytes were good mimics of real bryophytes (Table 2).

The entire data set obtained in each experiment at each site (15 samples) was also classified by TWINSPAN (Chapter 2). A maximum of seven indicator species were chosen to characterise each division, as too many weaken the polarisation and too few increase the chance of random classificatory errors (McCune 1987). Six divisions were performed on the data set.

Table 1: List of the 23 operational taxonomic units (OTU) previously shown to display strong habitat preferences for either bryophytes or riffles (Chapter 2). Abundances of these OTU were analysed for evidence of habitat preference amongst living and artificial bryophytes, and riffles. Brackets after certain OTUs indicate that they were restricted to one site: where no brackets occur, the OTU was found at both sites.

BRYOPHYTE TAXA	RIFFLE TAXA
Diptera:	Plecoptera:
Chironomidae - larvae	*Stenoperla prasina* (Newman) (Tim's Creek)
Chironomidae - pupae	*Zelandobius* sp.
Limonia hudsoni Edwards	
Muscidae sp. A (Tim's Creek)	Trichoptera:
Empididae sp. A (Tim's Creek)	*Oeconesus similis* McLachlan (Tim's Creek)
Empididae sp. B (Mouse Stream)	Ephemeroptera:
Austrosimulium ungulatum Tonnoir (Tim's Creek)	*Deleatidium* sp.
	Nesameletus sp.
Plecoptera:	Coleoptera:
Zelandoperla sp.	Helodidae sp. C (Tim's Creek)
Cristoperla fimbria (Winterbourn) (Tim's Creek)	
Acroperla spiniger (Tillyard) (Mouse Stream)	
Trichoptera:	
Hydrobiosis silvicola McFarlane (Mouse Stream)	
Zelolessica cheira McFarlane (Tim's Creek)	
Hydrobiosidae	
Coleoptera:	
Orchymontia sp. (Tim's Creek)	
Nematoda	
Copepoda	
Tardigrada	
Macrobiotis dispar (Murray) (Mouse Stream)	

Table 2: Summary of possible results of a comparison to ascertain whether artificial bryophytes were colonised by faunas more similar to those on living bryophytes than on riffles.

TAXA ANALYSED	OUTCOMES OF COMPARISON					
	Artificial v Bryophytes			Artificial v Riffles		
	1. Artificial < bryophytes	**2. Artificial > bryophytes**	**3. Artificial = bryophytes**	**1. Artificial < riffles**	**2.Artificial > riffles**	**3. Artificial = riffles**
A. Bryophyte - dwelling	mimic is bad; taxa characteristic of bryophytes do not colonize artificial structures.	mimic is good; but may over-estimate some taxa.	mimic is good; taxa characteristic of bryophytes colonize artificial structures as well.	mimic is bad; expect to get more taxa characteristic of bryophytes in artificial structures than riffles.	mimic is good; expect more taxa characteristic of bryophytes to occur in artificial structures.	mimic is bad; expect to see similar densities of bryophyte dwelling animals on real and artificial bryophytes.
B. Riffle - dwelling	mimic is good; taxa characteristic of riffles are not expected to colonize artificial structures.	mimic is bad; artificial structures contain more riffle dwelling taxa than real bryophytes.	mimic is good; taxa characteristic of riffles are expected to be absent from both real and artificial bryophytes.	mimic is good; expect to have fewer taxa characteristic of riffles colonizing artificial structures.	mimic is bad; expect to see fewer riffle dwelling taxa colonizing artificial structures.	mimic is bad; expect to see fewer riffle dwelling taxa colonizing artificial structures.

RESULTS

Habitat preference analysis

Total invertebrate densities within artificial bryophytes were similar to those amongst bryophytes and greater than those in stony riffles in both trials at Mouse Stream, but only in the first trial at Tim's Creek (Table 3). Average taxonomic richness per sample at Mouse Stream was similar in the three habitats in the first trial, but significantly fewer taxa were taken in stony riffles in the second (Table 3). At Tim's Creek, however, average taxonomic richness was similar in all three habitats in both trials (Table 3). Artificial bryophytes supported fewer taxa than natural substrates at both sites in trial 1, whereas similar numbers of taxa were collected from both artificial and living bryophytes in trial 2 at both sites (Table 3).

Comparison 1: Artificial and real bryophytes

Twenty three taxa, 17 characteristic of bryophytes and 6 of riffles, were analysed for preferences for or against artificial bryophytes (Table 1). In comparisons of artificial and natural bryophytes at Mouse Stream, artificial bryophytes were colonised by fewer *Limonia hudsoni* (Edwards), Empididae sp.B, and nematodes than their real counterparts. They thus represented poor bryophyte mimics for these taxa, in the case of the former at least because it eats mosses (Chapter Six). All other taxa characteristic of bryophytes colonised artificial bryophytes equally to, or better than living plants, suggesting that the mimics provided suitable living conditions for these taxa (Table 4a).

Nematodes also colonised artificial bryophytes in lower densities than real ones at Tim's Creek, whereas Empididae sp. B, *Zelandoperla*, larvae and pupae of Chironomidae and *Cristaperla fimbria* (Winterbourn) colonised these structures as well as, or better than the real plants (Table 4a).

Densities of the riffle dwelling mayfly, *Deleatidium*, at Mouse Stream were lower on artificial bryophytes than real ones in the first trial, but higher in the second trial (Table 4b). Artificial bryophytes also supported higher densities of the riffle-dwelling stonefly

Table 3: Total invertebrate density, average taxonomic richness and total taxa collected from the three substrates placed in each stream for a 2 month period in trials 1 and 2. *denotes significant difference (P <0.05) between substrates as determined by ANOVA, superscripts of the same value denote that the means of these samples are not significantly different (P <0.05), as determined by Tukey's Test.

	Trial	Riffles	Bryophytes	Artificial bryophytes	F-value
MOUSE STREAM					
Total invertebrate density (m^{-2})	1	13751	162 740[1]	71 360[1]	30.08*
	2	3 929	236 880[1]	180 580[1]	34.6*
Average taxonomic richness	1	2.8[1]	15.2[1]	13.6[1]	0.59
	2	8.8	20.8[1]	18.4[1]	6.68*
Total taxa collected	1	22	26	19	
	2	19	33	32	
TIM'S CREEK					
Total invertebrate density (m^{-2})	1	8 214	33 220[1]	41 360[1]	40.1*
	2	15 066[1]	42 400[1]	22 660[1]	3.31
Average taxonomic richness	1	15.8[1]	14.0[1]	13.2[1]	0.61
	2	23.4[1]	18.0[1]	15.0[1]	3.42
Total taxa collected	1	31	28	24	
	2	40	36	37	

Table 4: Results of Tukey's Tests following determination by ANOVA of habitat preferences of selected OTU in riffles, and on natural and artificial bryophytes. This indicated where invertebrate abundances differed significantly between habitats (P <0.05) and enabled taxa to be placed in one of the 3 possible outcomes: i.e., 1. Artificial < bryophytes; 2. Artificial > bryophytes; 3. Artificial = bryophytes. The table shows the results of two comparisons; Artificials v Bryophytes, and Artificials v Riffles. 4a = analysis of bryophyte dwelling taxa, 4b = analysis of riffle dwelling taxa; "*denotes that the outcome for a particular taxa was similar in both trials.

Table 4a: BRYOPHYTE TAXA

Artificials v Bryophytes		Artificials v Riffles	
MOUSE STREAM	TIM'S CREEK	MOUSE STREAM	TIM'S CREEK
1. Artificial < bryophytes		1. Artificial < riffles	
Limonia hudsoni	Nematoda	Nematoda	
Empididae sp. B			
Nematoda**			
2. Artificials > bryophytes		2. Artificials > riffles	
Acroperla spiniger	Empididae sp. B	Chironomidae larvae**	Chronomidae larvae**
	Zelandoperla	Chironomidae pupae	*Zelandoperla*
		*Zelandoperla***	Empididae sp. B
		*Acroperla spiniger**	
		Macrobiotis dispar	
		Copepoda	
		Nematoda	
3. Artificial = bryophytes		3. Artificial = riffles	
Chironomidae larvae**	Chironomidae larvae**	*Limonia hudsoni***	Nematoda
Chironomidae pupae**	Chironomidae pupae	Empididae sp. B	
Zelandoperla	*Cristaperla fimbria***	Hydrobiosidae	
Limonia hudsoni		Muscidae sp. A	
Macrobiotis dispar		Nematoda	
Muscidae sp. A			
Hydrobiosidae			
Copepoda			

Table 4b: RIFFLE TAXA

Artificials v Bryophytes		Artificials v Riffles	
MOUSE STREAM	TIM'S CREEK	MOUSE STREAM	TIM'S CREEK
1. Artificial < bryophytes		1. Artificial < riffles	
Deleatidium			*Deleatidium*** *Nesameletus*** *Stenoperla prasina***
2. Artificials > bryophytes		2. Artificials > riffles	
Zelandobius	*Zelandobius*	*Zelandobius*	
Deleatidium	*Stenoperla prasina*		
3. Artificial = bryophytes		3. Artificial = riffles	
Zelandobius	*Deleatidium* *Nesameletus* *Stenoperla prasina*	*Deleatidium* *Zelandobius*	*Zelandobius*

Zelandobius in the second trial, and in trial 1 at Tim's Creek. Densities of *Deleatidium*, *Nesameletus*, and *Stenoperla prasina* (Newman) were similar on real and artificial bryophytes at Tim's Creek in trial 1.

Although enhanced densities of these riffle dwelling taxa on the artificial substrates implies that they were poor mimics of real bryophytes, most of these animals were observed in the field to be primarily on the structure's base and on the underlying bedrock, and were consequently washed into the collection net during sampling. As they were not associated with the "stems" of the artificial bryophytes, their presence in the samples reflects a minor collection problem, and not a shortcoming of the bryophyte analogues.

Comparison 2: Artificial bryophytes and riffles

Densities of some bryophyte dwelling taxa (larval and pupal Chironomidae, *Acroperla spiniger* (Tillyard), *Zelandoperla*, *Macrobiotis dispar* (Murray), Copepoda and Nematoda) were all higher on artificial bryophytes than in riffles at Mouse Stream (Table 4b). Similarly, densities of larval Chironomidae, Empididae sp. B and *Zelandoperla* were higher on artificial bryophytes than in riffles at Tim's Creek (Table 4b). Thus the substrates were good mimics of real bryophytes for these taxa.

In contrast, however, densities of nematodes at both sites, and of *Limonia hudsoni*, Empididae sp. B, Muscidae sp. A and small Hydrobiosidae larvae at Mouse Stream were similar in riffles and on artificial bryophytes (Table 4b)

Densities at Mouse Stream of the normally riffle dwelling *Zelandobius* and *Deleatidium* on artificial bryophytes were greater than, or equal to those in riffles making these structures poor mimics (Table 4b). Densities of *Zelandobius* at Tim's Creek were also similar between artificial bryophytes and riffles, whereas densities of the riffle dwelling mayflies *Nesameletus* and *Deleatidium*, and the stonefly *Stenoperla prasina*, were all less within artificial bryophytes than riffles (Table 4b).

Organic matter content

The three habitat types sampled at Tim's Creek all contained greater quantities of large particulate organic matter (i.e., LPOM, CPOM) than their counterparts at Mouse Stream ($F = 8.52, 5.36$ in trial 1; $7.76, 5.56$ in trial 2 for LPOM and CPOM, respectively, $p < 0.05$). Quantities of the finer organic fractions (i.e., MPOM and FPOM) associated with natural and artificial substrates did not differ significantly between sites, however ($F = 0.55, 2.72$ trial 1; $0.21, 0.08$ trial 2 for MPOM and FPOM respectively, $p>0.05$).

Furthermore, at both sites, artificial mosses and stony substrata contained similar quantities of fine organic materials (i.e. materials < 0.5 mm; Table 5). Living bryophytes at both sites contained, and trapped, significantly more organic matter of all sizes, than either stony riffles or artificial mosses in trial 1. In trial 2, however, samples from all three habitats contained similar quantities of CPOM and MPOM at Mouse Stream, and of CPOM and FPOM at Tim's Creek (Table 5).

Temporal aspects of colonization

Invertebrate densities increased with time on artificial substrates set out weekly in Mouse Stream for 4 weeks, but fluctuated after this (Fig. 2). Algal biomass (as indicated by chlorophyll *a* concentration) increased to maximal values after 16 weeks, but this was not significantly different to accrual after four weeks (Fig. 2), indicating that most algal colonization occurred within 4 weeks. Quantities of trapped organic matter however continued to increase with exposure time, and reach highest biomass after 16 weeks (Fig. 2). Colonization by individual taxa was also rapid, with average and total taxonomic richness on artificial bryophytes exposed for 1 week ($x = 13.8$ for average, $x = 26$ for total taxonomic richness) being similar to that on structures set out for 16 weeks ($x = 17.0$ for average, $x=17$ for total taxonomic richness).

Community classification

Invertebrate assemblages in artificial moss samples were more similar to those on living bryophytes than in stony riffles, and were grouped together by the TWINSPAN analysis (e.g., Fig. 3). Samples collected from riffle areas in

Table 5: Quantities of organic matter collected from the three substrates in trials 1 and 2. *denotes significant differences ($P < 0.05$) between substrates as determined by ANOVA, superscripts of the same value denote that the means of these samples are not significantly different ($P<0.05$), as determined by Tukey's Test.

	Trial	Riffles	Bryophytes	Artificial bryophytes	F-value
MOUSE STREAM					
LPOM	1	46.8[1]	418.8	26.8[1]	20.80*
	2	5.0	210.5[1]	130.7[1]	10.85*
CPOM	1	18.3[1,2]	70.1[1]	8.3[2]	7.75*
	2	8.7[1]	18.8[1]	5.3[1]	2.82
MPOM	1	6.2[1]	41.8	6.6[1]	11.16*
	2	8.6[1]	17.8[1]	18.0[1]	2.14
FPOM	1	3.2[1]	28.5	8.6[1]	17.46*
	2	2.5[1]	23.3	7.8[1]	7.43*
TIM'S CREEK					
LPOM	1	99.4[1]	355.2[1,2]	136.2[2]	5.56*
	2	91.4[1]	207.5	95.4[1]	4.86*
CPOM	1	19.1[1,2]	62.7[1]	12.6[2]	5.83*
	2	24.6[1]	19.9[1]	10.8[1]	1.61
MPOM	1	15.5[1]	58.6	7.2[1]	17.97*
	2	16.3[1]	15.9[1]	4.0	4.27*
FPOM	1	7.3[1]	48.1[1,2]	12.5[2]	5.07*
	2	19.9[1]	9.4[1]	4.6[1]	1.28

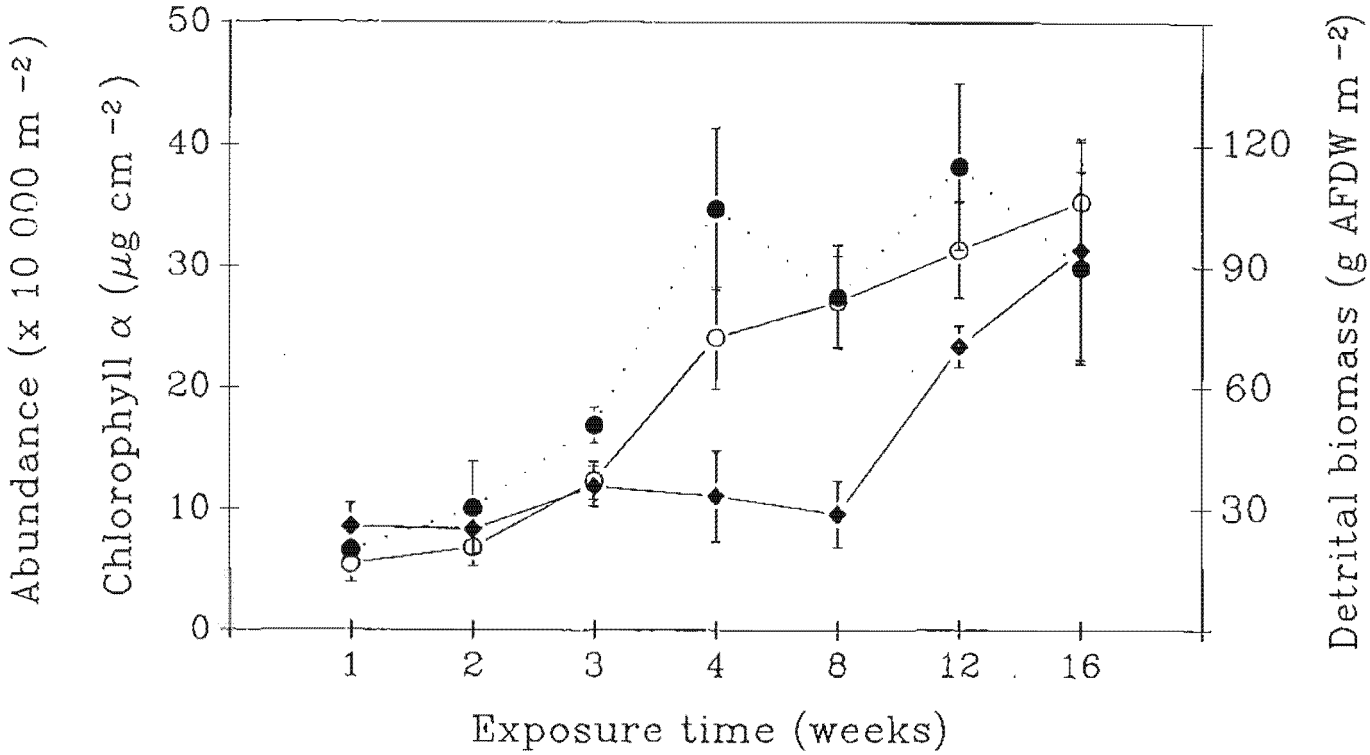


Fig.2: Quantities of selected parameters associated with artificial bryophytes that had been exposed at Mouse Stream for varying times to assess the time dependent effects of invertebrate and algal colonization and detrital entrappment (x ± 1SE, n = 5). Solid circles and dotted lines = total invertebrate abundance; open circles and solid lines = chlorophyll *a* concentration. Solid diamonds and dashed lines = trapped detrital biomass.

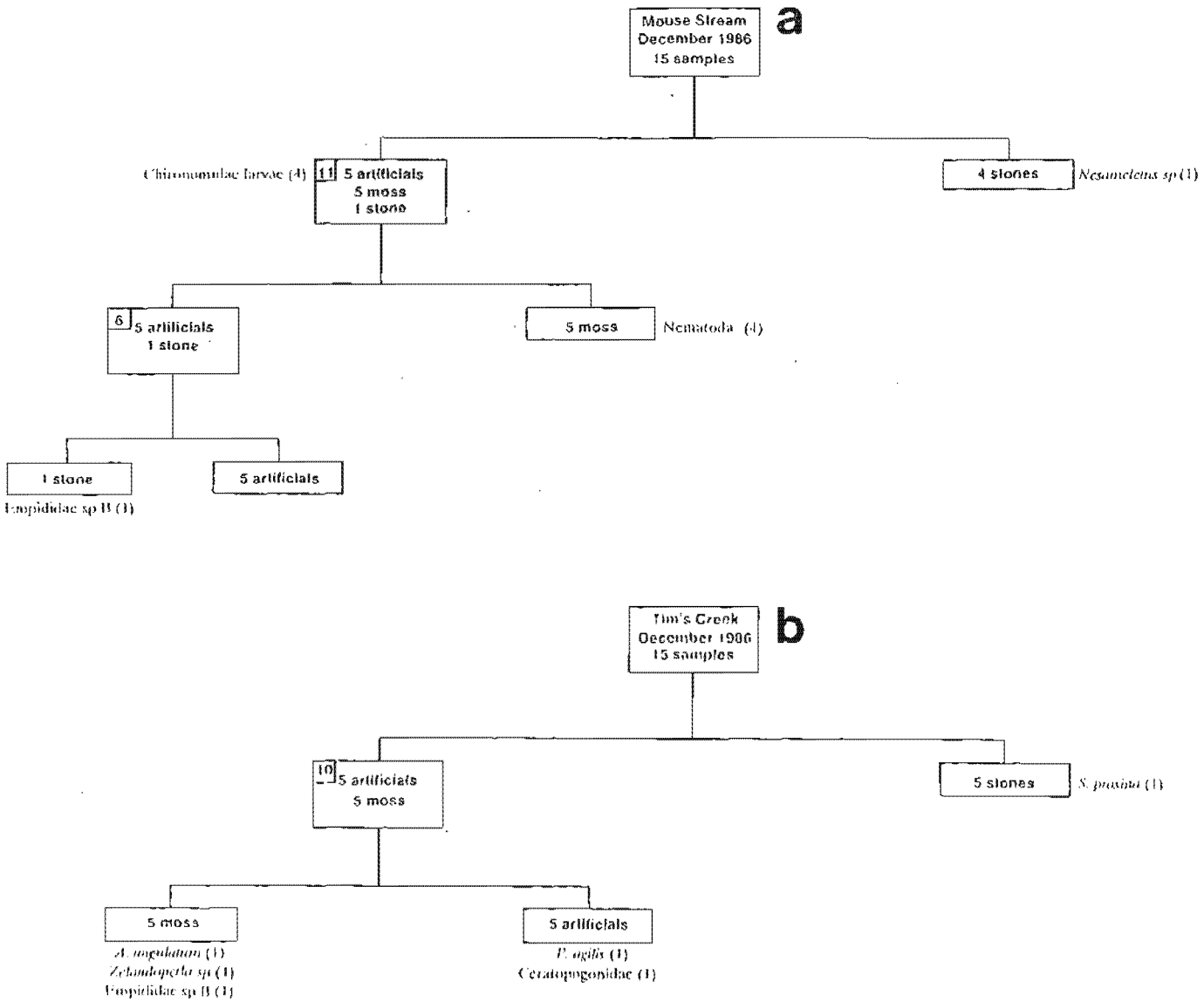


Fig.3: Examples of the dendrograms produced by TWINSPAN classification of samples collected from bryophyte and riffle habitats, and from artificial bryophytes in trial 1 at a). Mouse Stream; and b). Tim's Creek. The dendrogram shows the sample groupings produced at each TWINSPAN division, the number of samples in each grouping (small box) and a description of these samples (large box). Indicator species characteristic of samples within each sample grouping are presented, showing the taxa and its pseudospecies score (parentheses; see text).

both streams supported faunas that were distinct from those collected from natural or artificial bryophytes. Although the dichotomies produced by each TWINSPAN classification were different at each site in each trial, all artificial and natural bryophyte samples were classified into discrete groups, and were distinct from riffle samples.

DISCUSSION

Invertebrate colonization of artificial substrata was rapid, and reached a maximum after 4 weeks, following which invertebrate density fluctuated. Algal biomass similarly increased over time and although maximal values were reached after 16 weeks, periphyton development was not significantly increased after 4 weeks. Such rapid invertebrate colonization concurs with the observations of Meier *et al.* (1979), and Boothroyd & Dickie (1989) river who concluded that 39 and 28 days respectively allowed invertebrate densities to reach equilibrium with the surrounding environment. Similarly, Biggs (1988) found that maximal algal biomass occurred after 4 weeks in oligotrophic New Zealand rivers, after which time older algal growths began to slough off. However, biomass of trapped detritus appeared to increase throughout the study and had not reached maximal values even after 16 weeks. Increasing quantities of this material appeared to have little effect on the colonization dynamics of aquatic invertebrates, the densities of which did not increase significantly after 4 weeks.

Lamberti & Resh (1985) showed that quantities of bacteria, chlorophyll *a* and macroinvertebrates were similar on artificial and natural substrata exposed in a stream for 4 weeks, but considered an 8 week exposure period was preferable if the biological communities on artificial substrates were to more accurately mimic those on surrounding stones. Although I used an 8 week exposure period in this study, it was clear that invertebrate and algal colonization reached maximal values after 4 weeks. Thus the 8 week colonization period used in Mouse Stream and Tim's Creek was more than enough to ascertain whether living bryophytes were accurately mimicked by their artificial analogues.

Both the TWINSPAN analysis and the analysis of densities of individual taxa colonizing artificial bryophytes illustrated how the faunas of these structures resembled

those of living bryophytes more closely than those of stony riffles. Although densities of some taxa at Mouse Stream (i.e., Nematoda, *Limonia hudsoni* and an empidid) and at Tim's Creek (i.e., Nematoda) were lower on artificial bryophytes, total invertebrate abundances, species richness and abundances of 9 taxa characteristic of bryophytes at Mouse Stream, and 5 taxa at Tim's Creek, were little affected by replacement of real bryophytes with the artificial analogues.

This finding contrasts with that obtained in several previous investigations in which artificial plants always supported lower invertebrate densities (Glime & Clemons 1972, McKenzie-Smith 1987, Smith-Cuffney 1987, Cox 1988), and most likely reflects differences in exposure time of artificial substrates. Incubation times used range from 1 week (Cox 1988) to 4 weeks (McKenzie-Smith 1987, Smith-Cuffney 1987). Glime and Clemons (1972) incubated their substrata from 4-14 weeks, but analysed the combined data set. Thus, it is likely that these previous studies did not expose their artificial substrates long enough to enable maximal invertebrate densities, and detrital and algal biomass, to be reached.

Because current velocity is reduced within bryophyte mats, their detritus-trapping qualities are enhanced and materials are retained within their matrices (Johnson 1978, Maurer & Brusven 1983, Devantry 1987, Smith-Cuffney 1987). Reduced quantities of trapped particulate organic matter within the artificial bryophytes suggests that these structures lacked the necessary architecture of their living counterparts to effectively trap such material. Bryophyte stems and leaves often support dense periphyton assemblages however (Johnson 1978, Appendix 4), and high invertebrate densities within artificial bryophytes may therefore reflect high periphyton biomass associated with them (Glime & Clemons 1972, McKenzie-Smith 1987, Cox 1988).

Plant form has often been implicated as affecting invertebrate communities, and studies with macrophytes have shown how complex leaf morphology increases both periphyton density (Gregg & Rose 1985) and invertebrate numbers (Harrod 1964, Rooke 1984, 1986; but see Cyr and Downing (1988)). Growth forms of rheophilous bryophytes similarly affect invertebrate community composition, and indeed in a very early study, Percival & Whitehead (1929, 1930) observed that "thick moss" was dominated by oligochaetes whereas "loose moss" was dominated by Chironomidae. Similarly, Cox

(1988) argued that plant form was a strong factor in determining the taxonomic composition of the meiofauna associated with patches of two rheophilous bryophytes differing in growth form (*sensu* Glime 1968a); the mat-like *Eurhynchum riparioides* (Hedw.) Rich. and the streamer *Fontinalis novae-angliae* Sull.

The five dominant bryophytes in the study streams were all pleurocarpous and exhibited the mat growth pattern (Glime 1968a), gross morphology that was accurately mimicked by the artificial bryophytes. Thus it is unlikely that the absence of some taxa from these structures was a result of differences in "growth form" between natural and artificial bryophytes, but may reflect loss of the plant as food. For example, absence of *Limonia hudsoni* on the artificial bryophytes reflects its use of bryophytes as food (Chapter 6) and concurs with previous observations of consumption of bryophytes by some other larval tipulids (Alexander 1920, Bryce 1957, Brindle 1959, Byers 1961, Pritchard 1983).

Nematodes are also commonly found amongst bryophytes (Hynes 1961, Gerson 1972, Cox 1988) and species of Dorylaimoidea were abundant on mosses and liverworts in this study (and see Chapters 2 & 3). Free-living nematodes are primarily microbial feeders, consuming either algae, bacteria or fungi (Sohlenius 1979, 1980, Davis 1981). Fine particulate matter is also commonly consumed (Zullini & Ricci 1980, Hogue & Miller 1981) and indeed Cox (1988) found a positive correlation between nematodes and trapped FPOM amongst artificial mosses. Reduction in nematode density on artificial bryophytes may reflect either loss of a food source (moss), or reduced quantities of trapped FPOM and associated microbes within these structures.

Invertebrates also use bryophytes to construct shelters (Glime 1978), and larval *Zelolessica cheira* McFarlane frequently incorporate liverwort leaves in their cases (Cowley 1978, Appendix 4). Reduced densities of these caddis larvae on artificial bryophytes may reflect loss of such case construction material. Many insects also pupate on bryophytes (Glime 1968b, 1978, Gerson 1972), and chironomid pupae construct "pupation chambers" in leaf apices of *C. relaxa* and *B. blandum* (See Chapter 2 and Appendix 4). Densities of chironomid pupae were similar on artificial

and living bryophytes in this study, and on the former, "pupation chambers" were constructed between fibres making up strands of the artificial moss.

In contrast, stony riffles sampled in this study contained high densities of the common mayflies *Deleatidium* and *Nesameletus*, and the stoneflies *Stenoperla prasina*, *Austroperla cyrene* (Newman) and *Cristaperla fimbria*. Although densities of these invertebrates were occasionally high on artificial bryophytes, they were always seen on the undersides of the structures during collection and never between its "stems". Presumably animals here were obtaining shelter from water currents, or were grazing algal and detrital accumulations on either the substrates base or the bedrock below. Absence of these taxa from matrices of both real, and artificial bryophytes, probably reflects an inability to move freely amongst their tightly interwoven stems.

CONCLUSIONS

Both bryophytes and their artificial counterparts provide stable and permanent habitats for aquatic invertebrates in addition to plentiful food in the form of fine detritus and periphyton. The faunas colonizing living bryophytes and their plant analogues were very similar, the main differences being in the abundances of species that appear to use mosses and liverworts as food. This confirms the suitability of the artificial structures to accurately mimic natural bryophytes and to be colonised by a fauna similar to that which colonises the real plants, and supports their use in experimental manipulations designed to test the importance of accumulated detritus and algae to invertebrate colonists.

CHAPTER FIVE:

THE INFLUENCE OF ALGAE, DETRITUS AND SHELTER ON INVERTEBRATE COLONIZATION OF AQUATIC BRYOPHYTES

INTRODUCTION

Physical instability of New Zealand alpine streams often results in low organic matter retention rates (Graesser 1988), reduced density and diversity of benthic invertebrates (Rounick 1982, Rounick & Winterbourn 1982, Collier & Winterbourn 1987, Graesser 1988) and a fauna dominated by collector and browser functional feeding groups (Cowie 1980, Winterbourn *et al.* 1981).

Within these turbulent, high gradient, low order streams, aquatic bryophytes can proliferate and form extensive growths on stable boulders and bedrock. Benthic invertebrate populations associated with bryophytes are often greatly enhanced relative to those in stony riffles (e.g., Percival & Whitehead 1929, McElhone & Davies 1983, McKenzie-Smith 1987, Brusven *et al.* 1990), and certain invertebrate species often form characteristic associations with bryophytes (Chapter 2).

Bryophytes also act as a substrate for algal colonisation and detrital entrapment (Glime & Clemons 1972, Johnson 1978), and by doing so further increase the favourability of their environment for invertebrate colonisation. As a consequence, animal densities exceed those that might be expected solely on the basis of an increase in available surface area (McKenzie-Smith 1987). Whereas some bryophyte dwelling invertebrates consume bryophyte tissue (e.g., Alexander 1920, Byers 1961, Mutch & Pritchard 1984a,b, Willoughby & Mappin 1988, Wyatt & Stoneburner 1989), most invertebrates do not (Gerson 1972). Thus, invertebrate faunas associated with bryophyte analogues (artificial bryophytes) often closely resemble those amongst living bryophytes although abundance is typically often lower amongst mimics (Glime & Clemons 1972, McKenzie-Smith 1987, Smith-Cuffney 1987, Cox 1988, Chapter 2).

A reduction in abundance on mimics may be a consequence of lower quantities of detritus and periphyton associated with them compared with their living counterparts (Chapter 2). If so, this suggests that invertebrate colonisation is affected by their availability as food materials.

In this study, I examined invertebrate colonisation of different types of artificial substrata placed in two contrasting first order alpine streams, Mouse Stream and Tim's Creek. The substrata were designed to enable the importance of trapped detritus, periphyton biomass and available shelter in influencing colonisation to be assessed.

MATERIALS AND METHODS

1. Experimental substrata

"Full density" artificial bryophytes were constructed by weaving pieces of nylon twine (5 cm long, 1 mm thick) into squares (10 cm x 10 cm) of firm nylon mesh (pore size 4 mm). These substrata were anchored in place by tieing their leading and trailing edges to heavy weights that were buried in the substratum. All upstream weights were colour coded to indicate a particular treatment regime (Fig. 1). Importance of shelter was assessed by constructing four classes of artificial bryophytes with "stem" densities 1/2, 1/4 and 1/8 of the full density substrata. All artificial bryophytes were located on rock surfaces where bryophytes had been removed with a razor blade (Chapters 2 & 4).

In addition to artificial bryophytes, stone filled baskets were used to measure periphyton and detrital accrual. Baskets (15 cm x 15 cm x 5 cm) had walls and floors of 4 mm nylon mesh to facilitate movement of materials in and out of them, and were filled with stones that had been collected from each stream, autoclaved and washed free of organic material.

To determine appropriate size classes of stones to use in each stream, 10 Surber samples of substrate were taken from riffles at each site, and all inorganic contents collected were passed through a series of nested sieves (mesh sizes 4 cm, 2 cm, 1 cm, 0.5 cm). Trapped inorganic material on each sieve was weighed to determine the size-frequency of stones at each site. Subsequently, baskets were filled with stones in the proportions of those found naturally. Baskets were placed in depressions (5-10 cm deep) dug in riffles with the upper rims flush with the substratum. Materials removed were carefully replaced around each basket, thereby anchoring it.

2. Experimental manipulations

Four experiments were conducted to assess the affect of periphyton and trapped detritus on invertebrate colonisation. The first experiment assessed temporal relationships between algal, detrital and invertebrate colonisation of full density artificial bryophytes placed in each stream. The importance of shelter to invertebrates was assessed with artificial bryophytes of decreasing "stem" density. In addition, the importance of algal and detrital biomass in unstable riffles was investigated by examining colonisation of stone filled baskets. Following this, invertebrate colonisation dynamics of substrata with, and without high densities of algae and detritus were studied, to ascertain whether invertebrates tracked areas high in these materials.

(i) Temporal relationships: colonisation of artificial bryophytes

This experiment examined functional relationships between algal and detrital accumulation and invertebrate colonisation of artificial bryophytes. Ten replicate artificial bryophytes were placed in each stream in September 1987 (see no.(iv) below),

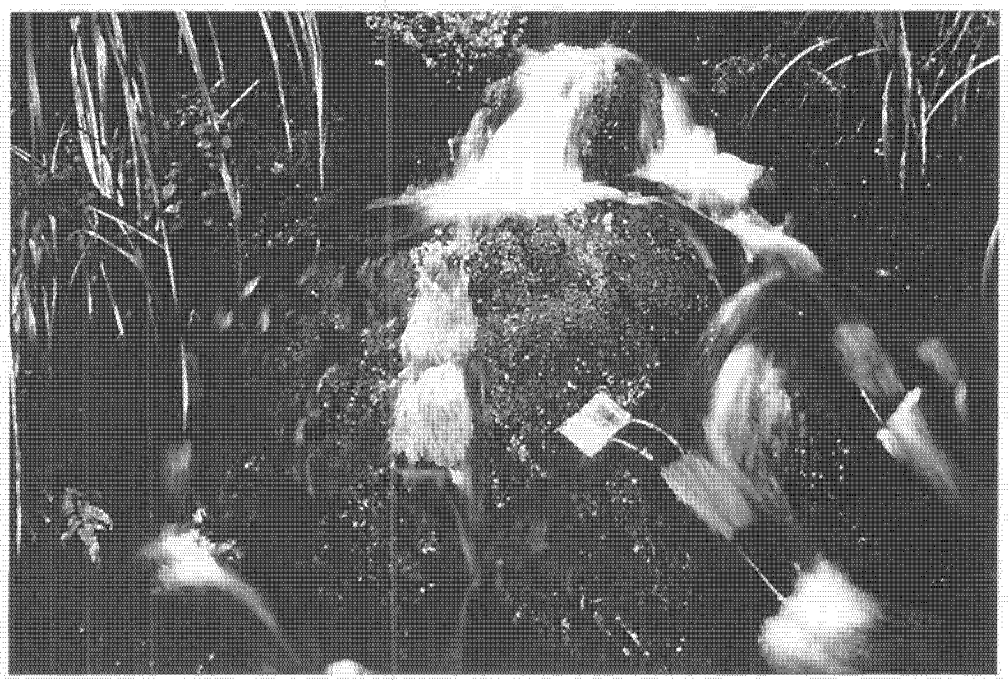


Fig. 1: Artificial bryophytes *in situ* at Tim's Creek during base flow. All substrates were located in bedrock areas from which all natural bryophyte growths had been removed with a razor blade.

and five more were set out in each of the following 3 months (October to December 1987). All substrata were successfully removed from Mouse Stream in January 1988, but sampling difficulties and loss of substrata as a result of floods forced me to abandon this experiment at Tim's Creek (Fig. 2a).

Following completion of the experiment at Mouse Stream, I placed artificial bryophytes in both streams at weekly, rather than monthly, intervals. The total duration of this trial was one month. Again, 10 replicate bryophyte analogues were initially placed at each site, and five more were set up in each of the following 3 weeks. This experiment was conducted at Mouse Stream in April-May 1988 whereas inclement weather meant the experiment was not conducted successfully at Tim's Creek until December 1989- January 1990 (Fig. 2a).

(ii) Importance of stem density as shelter

This experiment assessed the effect of shelter, i.e., "stem" density, on invertebrate colonisation of artificial bryophytes. Five replicates each of full and reduced density artificial bryophytes were placed in pairs in each stream for 2 months. Choice of pairs was determined by allocating them numbers which were drawn at random. This experiment was conducted concurrently with the first experiment, and substrata were sampled with the other samples at the experiment's conclusion.

(iii) Temporal relationships: colonisation of riffles

Five stone filled baskets were set out at each site at monthly intervals and those placed in Mouse Stream were successfully sampled in December 1987. The experiment was disrupted by floods at Tim's Creek but successfully conducted there from September 1989 to January 1990. In this latter trial, 10 baskets were set out in September, and 5 more in October, November and December. Five more were set out 2 weeks before all baskets were removed from Tim's Creek in January 1990 (Fig. 2b).

(iv) Importance of algae and detritus

To compare invertebrate colonisation of artificial bryophytes with and without periphyton and accumulated detritus, animals on five of the 10 substrata set out at the commencement of the first experiment were removed by placing each substrate into a 5 ppm solution of the insecticide/nematicide "Vydate"^{R} for 12 hours (Appendix 3). Substrata were then replaced in the stream from which they had been removed for a further month or week, along with new substrata to act as mimics without significant algal and detrital biomass (Fig. 2c). This experimental procedure was repeated with stone baskets placed at Tim's Creek. In this instance, five of the 10 baskets set out in September 1989 were treated with Vydate (5 ppm, 12 h) after they had been in the stream for 3 1/2 months. They were replaced for an additional 2 week exposure, along with newly placed baskets, representing habitats of low algal and detrital biomass (Fig. 2d).

A. TEMPORAL RELATIONSHIPS: COLONIZATION OF ARTIFICIAL BRYOPHYTES

4 months 3 2 1 SAMPLE — MOUSE STREAM (September 1987-December 1987)

4 weeks 3 2 1 SAMPLE — MOUSE STREAM (April-May 1988)

TIM'S CREEK (December-January 1990)

B. TEMPORAL RELATIONSHIPS; COLONIZATION OF STONE BASKETS

4 months 3 2 1 SAMPLE — MOUSE STREAM (September 1969-December 1987)

4 months 3 2 1 1/2 SAMPLE — TIM'S CREEK (September 1989 - January 1990)

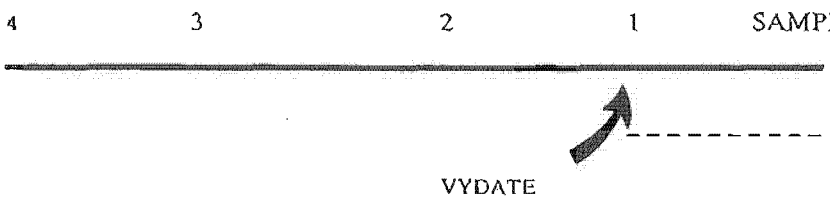
C. IMPORTANCE OF ALGAE AND DETRITUS: ARTIFICAL BRYOPHYTES — MOUSE STREAM (April-May 1988) TIM'S CREEK (December-January 1990)

1. CONTROL: 4 week exposure

4 3 2 1 SAMPLE — 4 weeks algal/detrital accumulation (▬▬) 4 weeks invertebrate colonization (- - - -)

Fig. 2: Outlines of sampling programs used at the two study sites to examine relationships between algal and detrital biomass, and invertebrate densites. In all colonization experiments, substrata were removed together (day labelled SAMPLE) although they were introduced to the streams at intervals shown (months or weeks): ▬▬= algal and detrital accumulation; - - - - - = invertebrate colonization.

2. VYDATED TREATED SAMPLES



4 weeks algal/ detrital accumulation (▬)
1 week invertebrate colonization (- - - -)

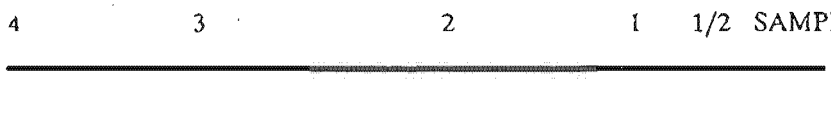
3. 1 WEEK EXPOSURE

1 week algal/ detrital accumulation (▬)
1 week invertebrate colonization (- - - -)

D. IMPORTANCE OF ALGAE AND DETRITUS: STONE BASKETS

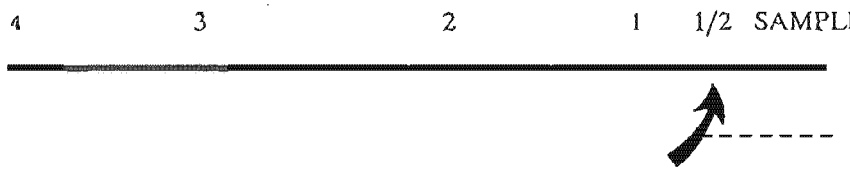
TIM'S CREEK (September - January 1990)

1. CONTROL: 4 month exposure



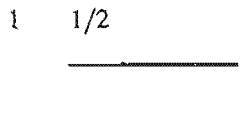
4 months algal/ detrital accumulation (▬)
4 months invertebrate colonization (- - - -)

2. VYDATE TREATED SAMPLES



4 months algal/ detrital accumulation (▬)
4 months invertebrate colonization (- - - -)

3. 2 WEEK EXPOSURE



2 week algal/ detrital accumulation (▬)
2 week invertebrate colonization (- - - -)

3. Sampling procedure and analysis

Each artificial bryophyte was removed by placing a Surber sampler (0.022 m^2) around it, cutting the strings attached to the anchoring weights, and pulling the structure into the collecting net (Chapter 4). Baskets were collected by carefully removing the stones surrounding them and lifting them clear of the substratum. A net (250 µm mesh) placed immediately downstream of the basket collected any material dislodged during removal, and the basket was placed into this net as it was removed from the water. Each basket and all material trapped in the collecting net were placed in plastic bags.

In addition to collecting all experimental substrata, five Surber samples were taken from bryophytes and stony riffles as previously outlined (Chapter 2) so that comparisons between experimental and natural communities could be made.

All samples collected were placed on ice in the field and returned to the laboratory where they were frozen (-18°C) pending analysis. Immediately after thawing, all substrata were analysed for total chlorophyll *a* and phaeopigment content. Substrata (either a single artificial bryophyte or the contents of each basket) were placed individually into Pyrex evaporating dishes (diameter 12 cm) and covered with 90% ethanol. The containers were sealed with thick PVC plastic film, placed in a water bath (80°C) and samples were left to boil for 10 minutes. After a 2 h incubation period (Appendix 2), 5 ml subsamples were withdrawn and filtered through Whatman GFC filters. Absorbances were measured at 665 and 750 nm (Uvicon spectrophotometer). Following acidification (0.5 M HCl, 1 h), absorbances were re-read and chlorophyll *a* and phaeopigment concentrations were calculated (Sartory & Grobbelaar 1984).

Following algal pigment determination, organic matter was separated from inorganic material that had accumulated amongst artificial bryophytes by elutriation through nested sieves (2.0 mm, 1.0 mm, 0.5 mm and 0.25 mm). These corresponded to the detrital size fractions of large, coarse, medium and fine particulate organic matter (LPOM, CPOM, MPOM and FPOM). Material trapped within artificial bryophytes was dislodged by application of high pressure water and by scrubbing with a stiff nylon brush before the sample was washed through the nested sieves.

All material on each sieve was placed in perspex Bogorov trays and invertebrates were identified and counted under a dissecting microscope (up to 100 x magnification). Material trapped on the 0.25 mm sieve was first decanted into a quadrapartite splitter and one subsample so obtained was examined in a smaller Bogorov tray (Chapters 3 & 4).

Following removal of invertebrates, remaining detritus was dried at 60 °C (48 h) and weighed. Ash free dry weight (AFDW) of each size fraction was determined after ashing in a muffle furnace (550 °C, 12 h).

4. Statistical Analysis

a. Community classification

Although invertebrate assemblages associated with artificial bryophytes were similar to those on living bryophytes (Chapter 4), the use of stone baskets to mimic natural riffles had not been validated. To determine whether invertebrate assemblages found on artificial substrata in the present experiments accurately mimicked their real counterparts, TWINSPAN analyses were conducted using invertebrate data sets for real and artificial bryophytes, riffles and stone-filled baskets that had been incubated for the longest time at each site. Abundance data were $\log_{10}(x+1)$ transformed and pseudospecies cut-levels were set at 0, 1, 2, 4 and 5 (Chapter 2).

b. Experimental analysis

For each sample I obtained quantitative data on organic matter AFDW (LPOM, CPOM, MPOM, and FPOM), algal pigment concentration (chlorophyll *a* and phaeopigments), total invertebrate abundance, taxonomic richness and the abundances of selected taxa. Differences in quantities of these variables in each experiment were assessed either by ANOVA or unbalanced ANOVA using PROC GLM (SAS 1988) following $\log_{10}(x+1)$ transformation. Where significant differences were observed, Tukey's Test was used to determine where these occurred (Zar 1974, SAS 1988).

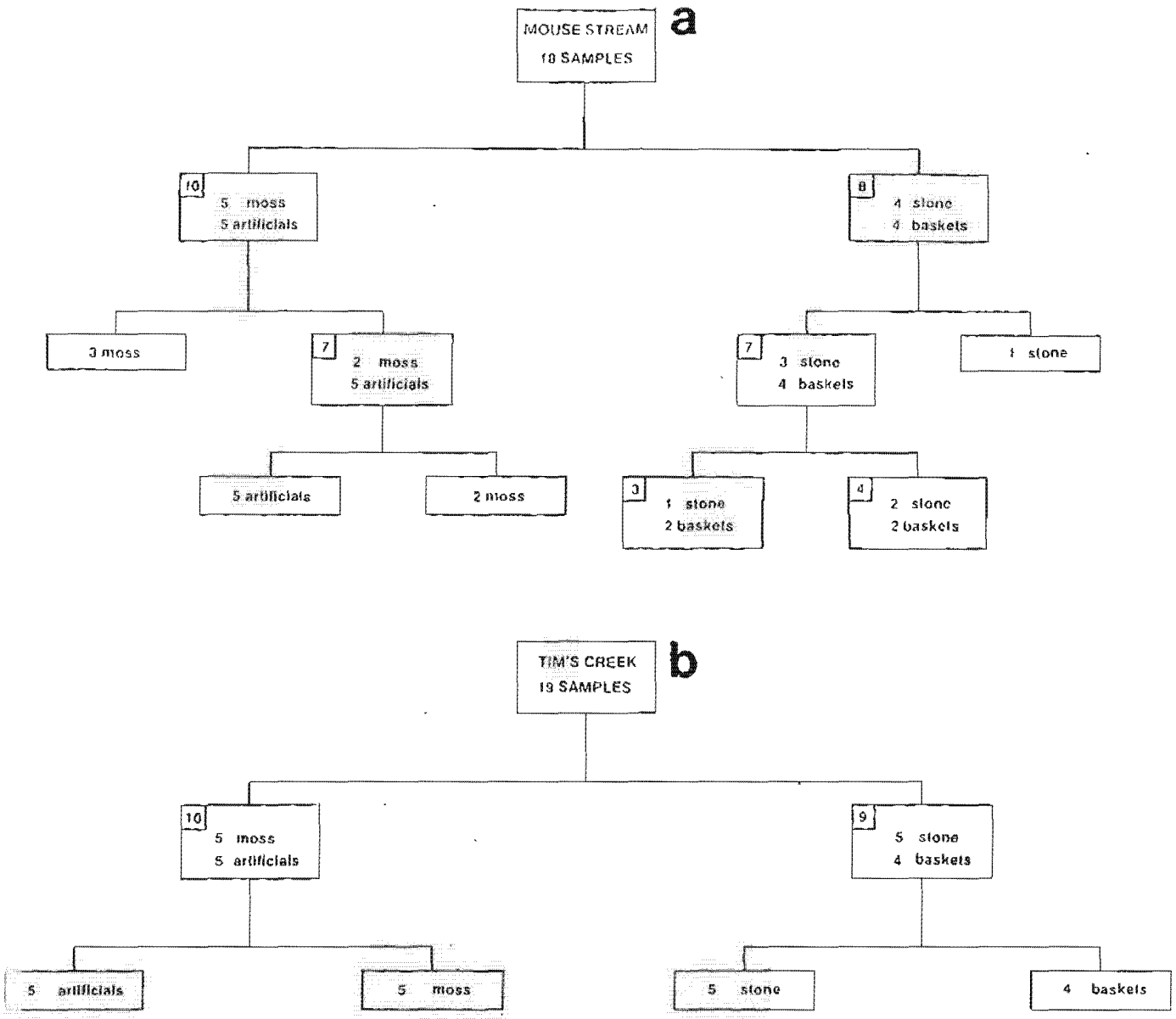
To assess effects of algae and detritus on invertebrate colonisation independent of time, variables associated with artificial bryophytes exposed for either 1 month or 1 week were compared (ANOVA or unbalanced ANOVA) with those associated with control and Vydate treated substrata that had been incubated for 4 months or 4 weeks.

Relationships between invertebrate abundance (total abundance and abundance of selected taxa) and environmental variables (algal pigment concentrations and detrital AFDW) were assessed by regression analysis using PROC STEPWISE (SAS, 1988). Only taxa that showed significant ($p<0.05$, PROC ANOVA; SAS 1988) density differences between substrata exposed for differing lengths of time in each experiment were analysed. Thus, predictive models were formulated to best describe the influence of algae and trapped detritus on invertebrate colonisation of artificial bryophytes and stone baskets, and by inference their real counterparts.

RESULTS

Community classification

Invertebrate assemblages associated with artificial bryophyte substrata and stone-filled baskets were more similar to their real counterparts than to each other. The first division in each TWINSPAN classification was based on habitat differences such that all samples from bryophytes (living and artificial) grouped together as did samples from riffles and



Figs 3a,b: TWINSPAN classifications of samples collected from bryophyte covered rocks, stony riffles, artificial bryophytes and stone-filled baskets that had been exposed for 1 and 4 months, respectively at Mouse Stream and Tim's Creek. Dendrograms show divisions produced by each TWINSPAN classification, the number of samples in each classification (small box) and a description of these samples (large box). a = Mouse Stream; b = Tim's Creek.

stone-filled baskets (Fig. 3b). Only after division 2 did samples collected from real bryophytes separate from their artificial analogues. Samples from riffles remained grouped with those from baskets until division 3. These results indicate that invertebrate assemblages associated with artificial substrata were similar to those in their respective natural counterparts (bryophytes and stony riffles).

(i) Temporal relationships: colonisation of artificial bryophytes

MOUSE STREAM

Artificial bryophytes exposed for 1, 2, 3 and 4 months differed with respect to the amounts of CPOM, MPOM and FPOM trapped within their matrices ($F= 4.53, 4.58, 4.79$, respectively, $p<0.01$, Fig. 4). These differences, however, were not positively correlated with exposure time as most material was trapped on substrata exposed for three months and least was on structures exposed for two. No differences were observed in quantities of algae colonizing each substrate ($F= 0.64$ for chlorophyll *a*, $F= 1.36$ for phaeopigment $p>0.05$) indicating that algal biomass peaked within 1 month of the substrata being set out in the stream.

In contrast, artificial bryophytes exposed weekly for 1 month were colonised by more algae after four weeks than one ($F= 6.69$ for chlorophyll *a*, $F= 8.27$ for phaeopigment, $p<0.01$, Fig. 5a). However, similar amounts of detrital biomass were found each week ($F= 0.94, 2.15, 2.15, 3.06$ for LPOM, CPOM, MPOM, FPOM respectively, $p>0.05$).

Total invertebrate abundance on mimics exposed monthly for 4 months did not increase with time, and was similar on living and artificial bryophytes ($F= 1.96$, $p>0.05$). Furthermore, densities of only 6 of the 22 taxa selected for analysis differed between substrata: in all cases higher densities were on living bryophytes.

Total invertebrate abundance, and the abundances of larval and pupal chironomids, tardigrades, nematodes and copepods were lowest on substrata exposed for 1 week and highest on substrata exposed for 4 weeks, or on natural bryophytes (Figs 5 b,c,d).

Invertebrate abundance within artificial bryophytes exposed monthly for 4 months was not significantly correlated with any measured environmental parameter. Although abundances of most taxa (3) were correlated with FPOM biomass and phaeopigment concentration (Table 1), the calculated regression models all had low predictive powers, with the variation in *Hydroblosis silvicola* McFarlane abundance being explained best (39%).

Of the environmental data collected from substrata exposed weekly for 4 weeks, densities of seven taxa were significantly correlated to CPOM biomass, and six taxa to FPOM biomass (Table 1). Biomass of LPOM was correlated to only 1 taxon (Table 1). Twenty four percent of the variation in abundance of *Zelandobius* larvae was

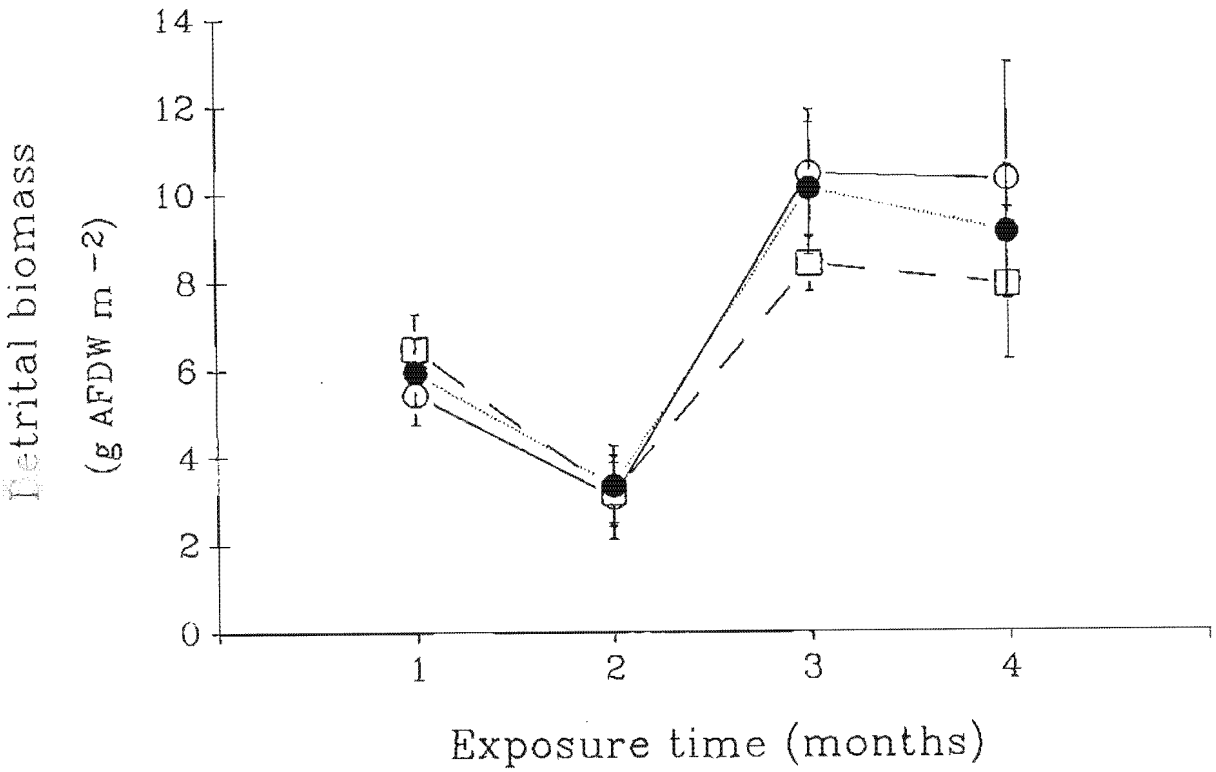


Fig. 4: Quantities of detritus trapped by artificial substrates exposed for 1, 2, 3 and 4 months at Mouse Stream ($\bar{x} \pm 1$ SE, n = 5). Open circles and solid lines = CPOM; filled circles and dotted lines = MPOM; open squares and dashed lines = FPOM.

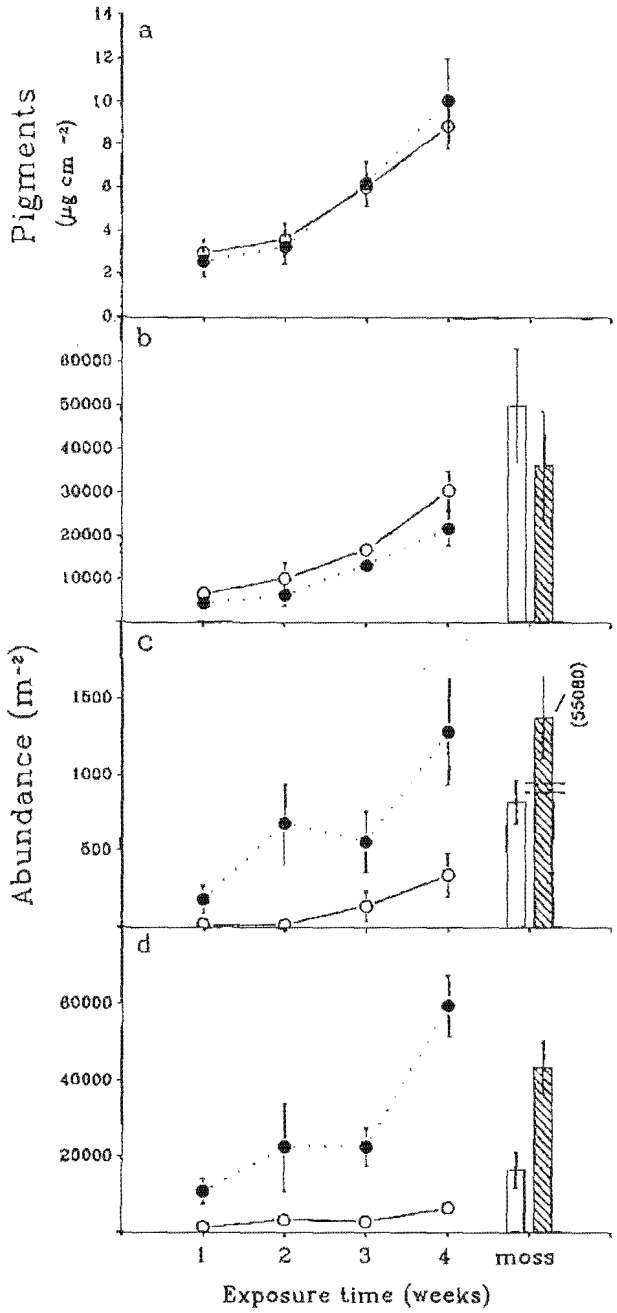


Fig. 5a: Concentrations of chlorophyll *a* and phaeopigments extracted from algae colonizing artificial bryophyte substrates exposed for 1, 2, 3 and 4 weeks at Mouse Stream ($\bar{x} \pm 1$ SE, n=5). Open circles, solid lines = chlorophyll *a*; filled circles, dotted lines = phaeopigments.

Figs 5b-d: Densities of invertebrates colonizing artificial bryophytes exposed for 1, 2, 3 and 4 weeks at Mouse Stream ($\bar{x} \pm 1$ SE, n=5).

b: total invertebrate density (open circles and bar) and larval chironomid density (closed circles and striped bar).

c: densities of pupating chironomids (open circles and bar) and nematodes (closed circles and striped bar).

d: densities of tardigrades (open circles and bar) and copepods (closed circles and striped bar).

Table 1: Numbers of taxa that were significantly correlated to the seven measured environmental variables associated with artifical substrates at Mouse Stream, as determined by stepwise multiple regression analysis. Taxa for the analysis (n) were chosen on the basis of exhibiting significant differences in density between experimental substrata.

Experimental treatment	Taxa analysed (n)	LPOM	CPOM	MPOM	FPOM	Chlorophyll *a*	Phaeopigments	Time (Shelter)
monthly mosses	6	1	1	2	3	1	3	0
weekly mosses	12	1	7	3	6	5	2	3
shelter mosses	10	1	4	2	3	2	3	3
stone-filled baskets	12	4	3	1	6	3	2	3

accounted for by CPOM (Table 2a), whereas FPOM accounted for 67% of the variation in chironomid abundance and 49% of the variation in copepod abundance. Sixty three percent of the variation in *Acroperla spiniger* (Tillyard) density was explained by phaeopigment concentration.

Total invertebrate abundance, and abundance of chironomid larvae were well explained by the total stepwise regression equation (90% and 87%, respectively). Stepwise regression also explained over 60% of the abundances of copepods, pupating chironomids and *A. spiniger* (Table 2a), with FPOM and algal pigments (chlorophyll *a* and phaeopigments) being major determinants.

TIM'S CREEK

Chlorophyll *a* concentrations increased significantly over time on artificial bryophytes exposed for 4 weeks ($F= 10.34$, $p<0.001$, Fig. 6a). No temporal differences in either phaeopigment concentration ($F= 1.83$, $p>0.05$) or detrital biomass were observed, however ($F= 1.91, 1.86, 2.34, 2.73$ for LPOM, CPOM, MPOM, FPOM, respectively, $p>0.05$).

Densities of only six of the 33 taxa analysed were significantly different between experimental substrata and living plants. Of these, the stonefly *Spaniocerca zelandica* (Tillyard), a larval empidid, and nematodes were present in higher densities after 4 than 1 week ($F= 2.87, 2.68, 4.12$, $p<0.05$; Figs 6 b,c). A similar pattern was observed for total invertebrate density ($F= 3.05$, $p<0.05$; Fig. 6d). Larval *Austroperla cyrene* (Newman) (Plecoptera) and *Limonia hudsoni* (Edwards) (Tipulidae) were more abundant on living bryophytes than artificial ones, as was taxonomic richness ($F= 8.52, 4.34, 4.44$ respectively, $p<0.01$; Figs 6 e,f).

Measured environmental parameters explained the abundances of five of the six taxa analysed. Of these, biomass of LPOM, CPOM, FPOM and time were correlated with the densities of two taxa, whereas abundances of only 1 taxon were correlated to MPOM biomass and phaeopigment concentration (Table 3). However, total coefficients of variation for each taxon were low, with FPOM being the most powerful predictor variable, yet it explained only 51% of the variance in density at best (Table 4a). Abundances of an empidid and an oribatid mite were best explained by the calculated stepwise regression equation (58% variation explained), whereas densities of other taxa, total invertebrate density, and taxonomic richness were poorly correlated with measured variables (Table 4a).

Tables 2a-c: The percentage of the variation in abundance of selected taxa on artificial substrates at Mouse Stream explained by each of 7 environmental variables entered in a stepwise multiple regression model. Only those taxa for which the total relationship explained >50% of density variation are presented.

a = artificial bryophytes set out weekly
b = reduced shelter artificial bryophytes
c = stone-filled baskets set out monthly

TABLE 2a

	DETRITAL BIOMASS				PERIPHYTON BIOMASS			
Taxa	LPOM	CPOM	MPOM	FPOM	Chlorophyll a	Phaeopigments	TIME	TOTAL VARIANCE
Chironomidae (larvae)		2.6		67.4	4.9	12.5		87.4
Chironomidae (pupae)		7.5		17.5	39.3			64.3
Acroperla spiniger						63.3		63.3
Tardigrada		12.1		34.7	8.7			55.5
Copepoda		10.2		49.3	10.1			69.5
TOTAL ABUNDANCE		4.1		70.4	1.8	13.4		89.7
TAXONOMIC RICHNESS		69.2					7.6	76.8

TABLE 2b

	DETRITAL BIOMASS				PERIPHYTON BIOMASS			
Taxa	LPOM	CPOM	MPOM	FPOM	Chlorophyll a	Phaeopigments	Shelter	TOTAL VARIANCE
Limonia hudsoni		61.2						61.2
Chironomidae (larvae)	15.1				55.1			70.1
Zelandobius				15.6		10.1	38.3	64.0
Tardigrada			53.7	16.2				69.9
Copepoda		6.9		45.1				52.0
TOTAL ABUNDANCE	13.1					54.4	4.9	72.8

TABLE 2c

	DETRITAL BIOMASS				PERIPHYTON BIOMASS			
Taxa	LPOM	CPOM	MPOM	FPOM	Chlorophyll a	Phaeopigments	TIME	TOTAL VARIANCE
Limonia hudsoni	18.7			45.7				64.4
Chironomidae (larvae)					6.0		66.7	72.7
Deleatidium	10.5	58.2		4.6		4.9		78.2
Zelandobius		53.3						53.3
Hydrobiosis silvicola			78.9					78.9
Copepoda	8.0			64.8		5.1		77.9
Ostracoda	25.4	1.7		54.8	4.7		5.1	91.7
TOTAL ABUNDANCE		7.1					71.2	78.3
TAXONOMIC RICHNESS		77.9					5.4	83.3

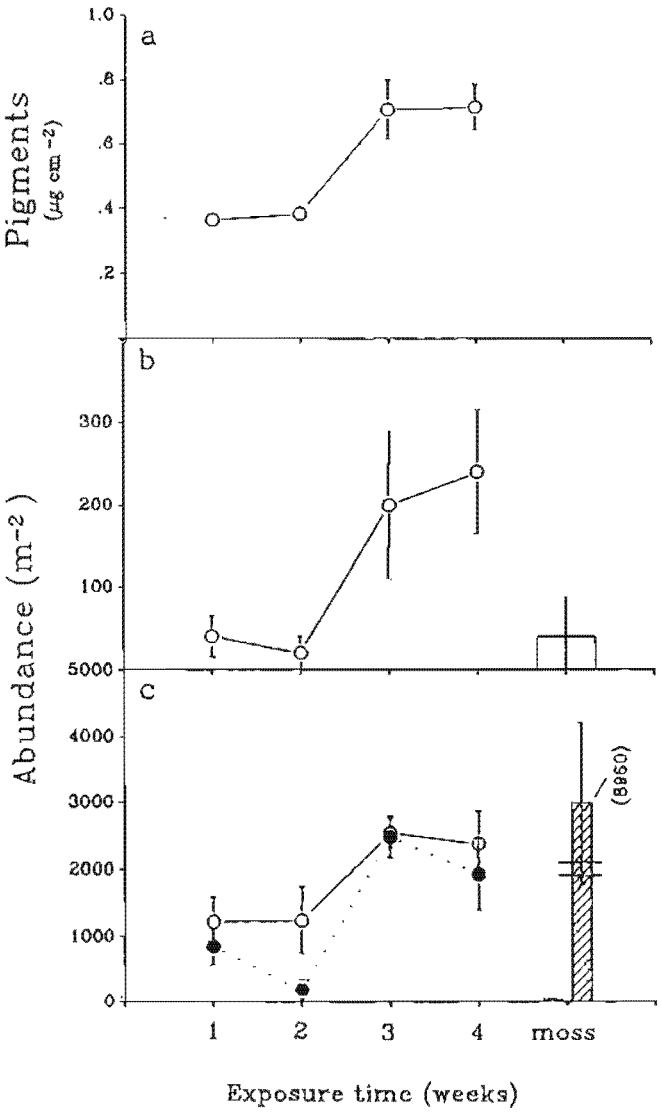


Fig. 6a: Concentrations of chlorophyll *a* extracted from algae colonizing artificial bryophytes exposed for 1, 2, 3 and 4 weeks at Tim's Creek (x ± 1 SE, n=5).

Figs 6b-f: Densities of invertebrates colonizing artificial bryophytes exposed for 1, 2, 3, and 4 weeks at Tim's Creek (x ± 1 SE, n=5).

b: density of *Spaniocerca zelandica* larvae.

c: densities of an empidid larva (open circles and bar) and nematodes (closed circles and striped bar).

d: total invertebrate density.

e: densities of larval *Austroperla cyrene* (open bars) and larval *Limonia hudsoni* (striped bars).

f: taxonomic richness.

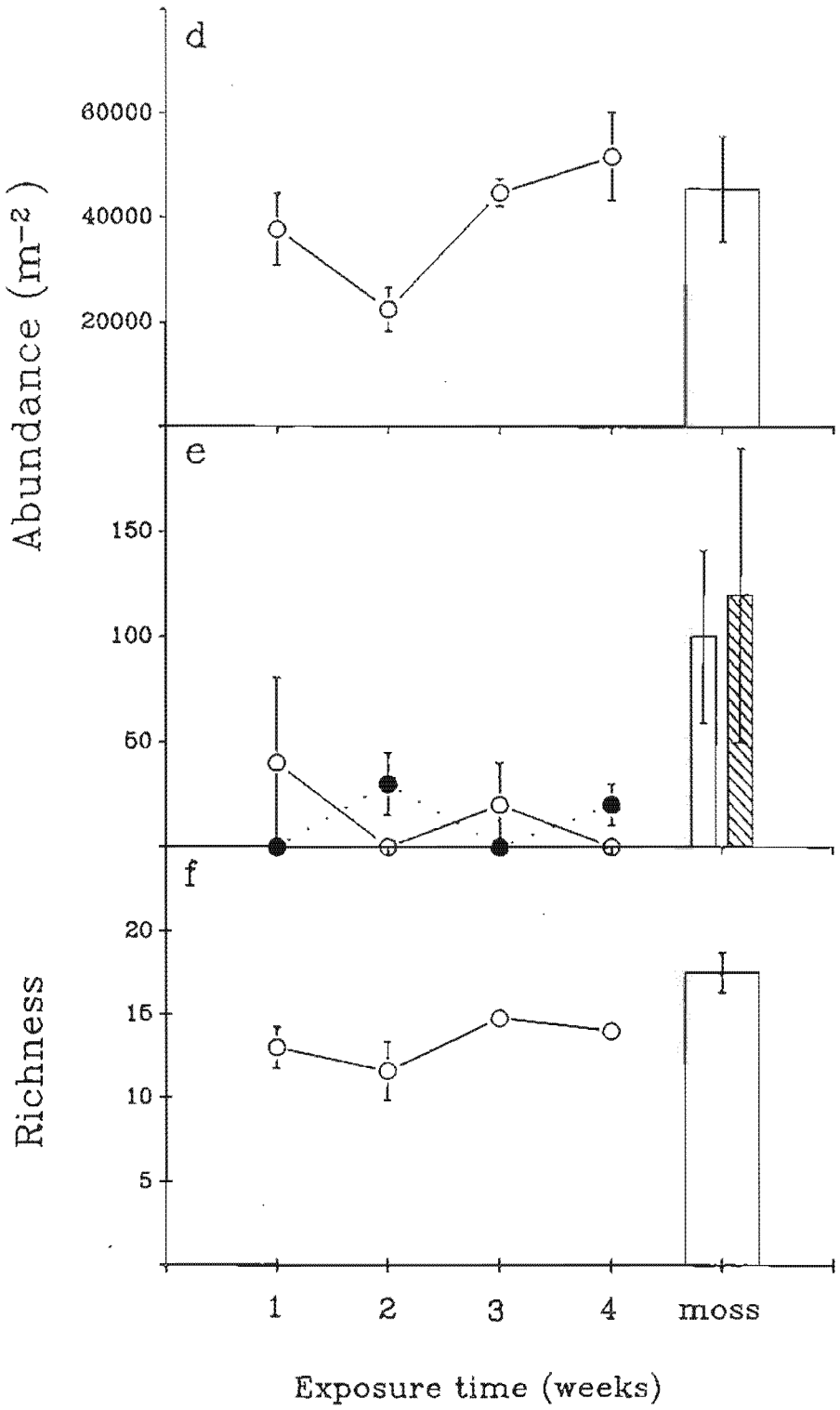

d
60000
40000
20000
Abundance (m-2)
e
150
100
50
f
20
15
10
5
Richness
1
2
3
4
moss
Exposure time (weeks)

Table 3: Numbers of taxa that were significantly correlated to the seven measured environmental variables associated with artifical substrates at Tim's Creek, as determined by stepwise multiple regression analysis. Taxa for the analysis (n) were chosen on the basis of exhibiting significant differences in density between experimental substrata.

Experimental treatment	Taxa analysed (n)	LPOM	CPOM	MPOM	FPOM	Chlorophyll *a*	Phacopigments	Time (Shelter)
weekly mosses	5	2	2	1	2	0	21	2
shelter mosses	4	0	2	3	1	1	1	1
stone-filled baskets	8	2	1	3	3	3	5	1

(ii) Importance of stem density as shelter

MOUSE STREAM

Quantities of algae and trapped detritus did not differ significantly between artificial bryophytes of different stem density (F= 0.58, 0.49, 0.54, 1.85 for LPOM, CPOM, MPOM, FPOM, respectively; F= 1.11, 0.73 for chlorophyll *a* and phaeopigment, respectively; p>0.05).

Total invertebrate density and taxonomic richness were highest on real mosses, however, and decreased with decreasing stem density (F= 3.78 total abundance, F= 7.77 taxonomic richness, p<0.01; Figs 7 a,b). Similarly, larvae of the caddisfly *H. silvicola*, Hydracarina, tardigrades, copepods and ostracods were significantly more abundant on living bryophytes and displayed a negative relationship with decreasing stem density of artificial bryophytes (Figs 7 c,d,e).

Presence of CPOM influenced the abundances of four of the ten taxa analysed (Table 1), and explained 61% of the variation in abundance of *L. hudsoni*. Other important predictor variables were MPOM, and chlorophyll *a*, which explained over 50% of variation in tardigrade and chironomid abundance respectively (Table 2b). Shelter explained 38% of the variation in *Zelandoblus* abundance, but only 10% of the variation in *A. spiniger* abundance.

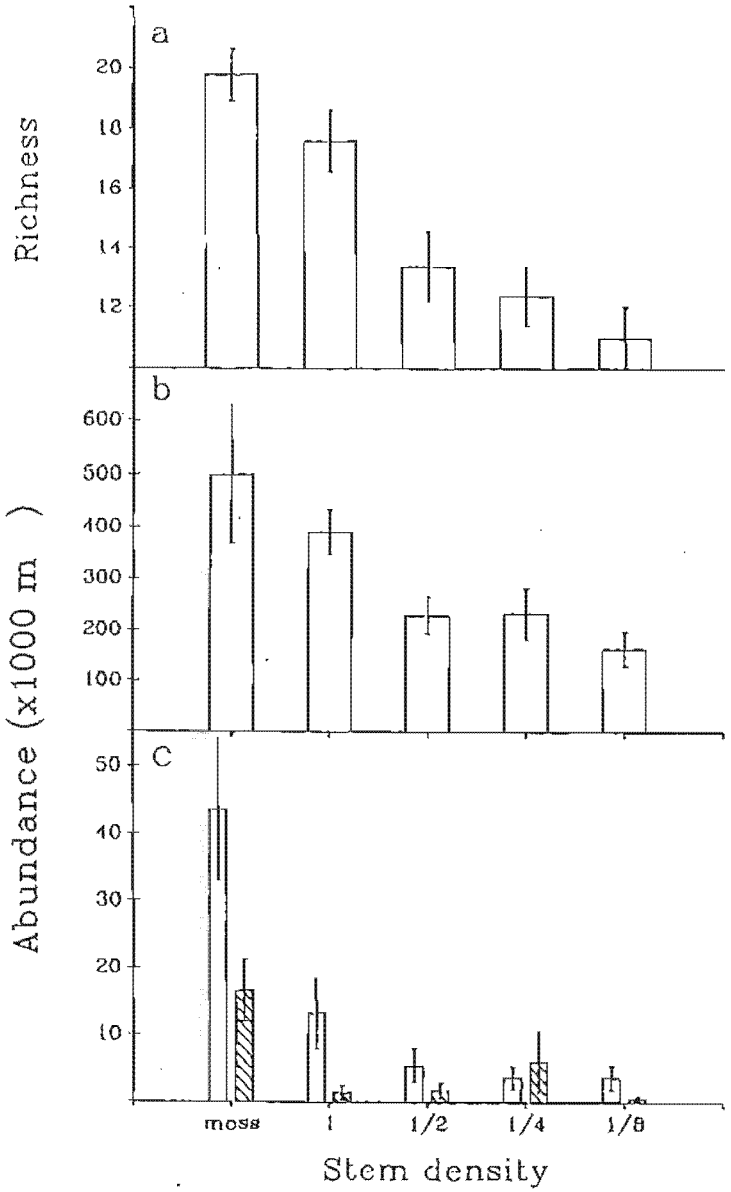
Calculated regression models for certain taxa explained over 60% of the variation in abundance of *Limonia hudsoni, Zelandoblus*, tardigrades and chironomids (Table 2b).

TIM'S CREEK

As at Mouse Stream, chlorophyll *a* and phaeopigment concentrations were unaffected by stem density of artificial bryophytes (F= 0.94, 2.19 for chlorophyll *a* and phaeopigment; p>0.05). However, less organic matter of all size fractions (except LPOM) was trapped on substrata with lower stem densities (F = 3.83, 4.28 and 5.84 for CPOM, MPOM and FPOM p<0.05, Fig. 8a).

Total invertebrate density, and densities of chironomids and nematodes differed significantly between treatments (F= 4.28, 4.43, 8.56, p<0.01; Figs 8 b,c,d) and were greatest on living bryophytes and full density analogues. Taxonomic richness, and densities of *A. cyrene* were also highest on living bryophytes (F= 7.08, 4.58; p<0.01), but were unaffected by reductions in stem density. The tipulid *L. hudsoni* and adult Elmidae (Coleoptera) were most common on living bryophytes (F= 2.98, 4.84; p<0.05), but absent from all but full density artificial bryophytes.

Densities of only four taxa analysed showed significant correlations with measured environmental parameters. MPOM was significantly correlated with three taxa, CPOM with two, and FPOM biomass, chlorophyll *a* and phaeopigment concentrations, and shelter with one (Table 3).



Figs 7a-e: Densities and taxonomic richness of invertebrates colonizing artificial bryophytes of decreasing stem density set out for 2 months at Mouse Stream ($\bar{x} \pm$ 1 SE, n=5).

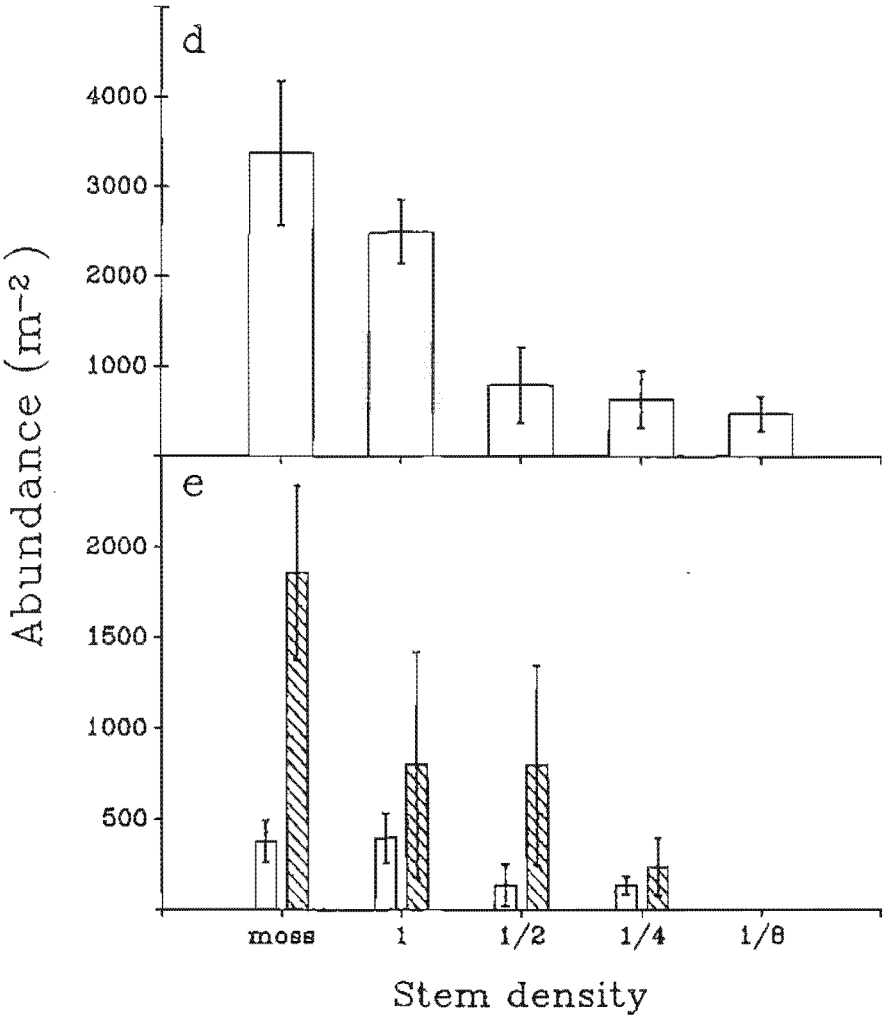
a: taxonomic richness.

b: total invertebrate density.

c: densities of copepods (open bars) and tardigrades (striped bars).

d: density of aquatic mites.

e: densities of *Hydroblosis silvicola* (open bars) and ostracods (striped bars).


d
4000
3000
2000
1000
e
2000
1500
1000
500
Abundance (m-2)
moss
1
1/2
1/4
1/8
Stem density

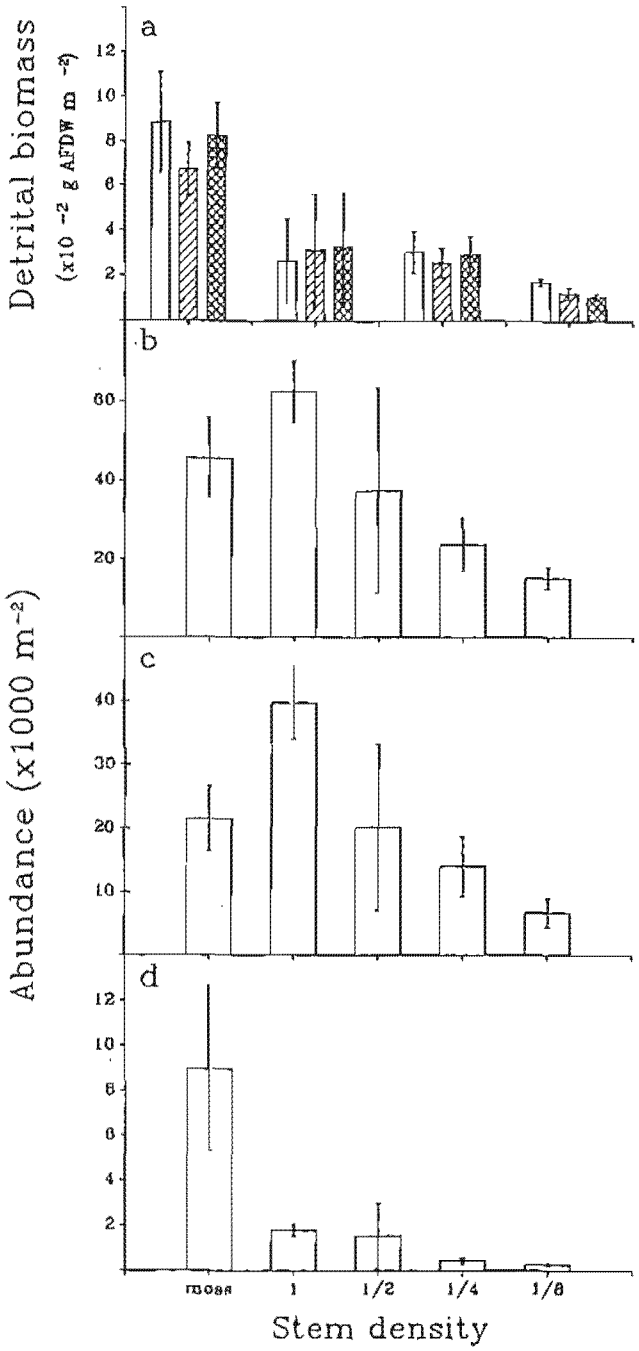


Fig. 8a: Quantities of detritus trapped by artificial bryophytes of decreasing stem density exposed for 2 months at Tim's Creek (x ± 1 SE, n=5). Open bars = CPOM; striped bars = MPOM; hatched bars = FPOM.

Figs 8b-d: Densities of invertebrates colonizing artificial bryophytes of decreasing stem density set out for 2 months at Tim's Creek (x ± 1 SE, n=5).

b: total invertebrate density.

c: density of chironomid larvae.

d: density of nematodes.

Tables 4a-c: The percentage of the variation in abundance of selected taxa on artificial substrates at Tim's Creek explained by each of 7 environmental variables entered in a stepwise multiple regression model. Only those taxa for which the total regression explained >50% of density variation are presented.

a = artificial bryophytes set out weekly
b = reduced shelter artificial bryophytes
c = stone-filled baskets set out monthly

TABLE 4a

	DETRITAL BIOMASS				PERIPHYTON BIOMASS			
Taxa	LPOM	CPOM	MPOM	FPOM	Chlorophyll a	Phaeopigments	TIME	TOTAL VARIANCE
Empididae sp. A				51.0		8.0		59.0
Oribatidae sp. A	7.0	23.2	10.4			18.3		58.9

TABLE 4b

	DETRITAL BIOMASS				PERIPHYTON BIOMASS			
Taxa	LPOM	CPOM	MPOM	FPOM	Chlorophyll a	Phaeopigments	Shelter	TOTAL VARIANCE
Empididae sp. B		50.2	19.1					69.3
Chironomidae (larvae)			72.3			7.1	4.2	83.6
Nematoda		6.1	72.5					78.6
TOTAL ABUNDANCE		4.3	71.0			6.5		81.7
TAXONOMIC RICHNESS			7.6	9.1	57.0	5.3		79.0

TABLE 4c

	DETRITAL BIOMASS				PERIPHYTON BIOMASS			
Taxa	LPOM	CPOM	MPOM	FPOM	Chlorophyll a	Phaeopigments	TIME	TOTAL VARIANCE
Paralimnophilia skusei			13.3	26.1	13.5	31.7		84.6
Ceratopogonidae			50.3					50.3
Chironomidae (larvae)					8.7	56.2		64.9
Deleatidium						50.6		50.6
Spaniocerca zelandica	3.5	81.0		4.6				89.1
Copepoda				5.0	8.1	63.3		76.4
Zelandobaetella maias	18.0		15.8				20.1	53.9
Oribatidae sp. A			82.4					82.4
TOTAL ABUNDANCE			11.3	8.7		69.1		89.1
TAXONOMIC RICHNESS			66.0			5.3		71.3

MPOM had the highest predictive power, and explained over 70% of the variation in total invertebrate, nematode and chironomid densities (Table 4b). Chlorophyll *a* explained 57% of the variation in taxonomic richness, and 50% of the variation in empidid densities was attributed to CPOM. Stepwise regression models had high predictive powers, with over 69% of the variation in chironomids, empidids, nematodes, total invertebrate density and taxonomic richness being explained (Table 4b). Degree of stem shelter explained only 4.2% of the variation in larval chironomid abundances.

(iii) Temporal relationships: colonisation of riffles

MOUSE STREAM

The amount of trapped detritus and algae present in stone-filled baskets exposed for 1, 2, 3 and 4 months increased over time ($F= 7.18$ and 6.28 for CPOM and FPOM; $F= 9.43$ and 8.77 for chlorophyll *a* and phaeopigment; $p<0.01$, Figs 9 a,b).

Of the 22 riffle dwelling taxa analysed, densities of only larval and pupal chironomids, the mayfly *Deleatidium* and the stonefly *Zelandobius* were significantly higher in baskets than natural riffles ($F= 7.04$, 11.66, 3.98, and 5.57, respectively; $p<0.05$; Figs 9 c,d,e). In contrast, natural riffles supported higher densities of nematodes and ostracods than baskets, although densities continued to increase in the latter with time (Fig. 9f).

FPOM biomass was strongly correlated with the abundances of six of riffle taxa (Table 1). This variable accounted for 65% and 55% of the variation in abundances of copepods and ostracods (Table 2c). Variation in invertebrate abundance was also related to CPOM biomass, which accounted for 58% and 53% of the variation in *Deleatidium* and *Zelandobius* abundances, MPOM biomass which explained 79% of the variation of *H. silvicola* abundance, and time which explained 68% of the variation in chironomid abundance.

Calculated regression models for individual taxa had high predictive power, with 92% of the variation in abundance of ostracods being accounted for, and over 70% of the variation in abundances of larval chironomids, *H. silvicola*, *Deleatidium* and copepods (Table 2c).

TIM'S CREEK

Quantities of algae and detritus in stone filled baskets generally peaked after 3 or 4 months ($F= 3.22$, $p<0.05$ for chlorophyll *a*; $F= 7.93$, 6.01, 8.79, 4.56 for LPOM, CPOM, MPOM, FPOM; $p<0.05$; Figs 10 a,b,c).

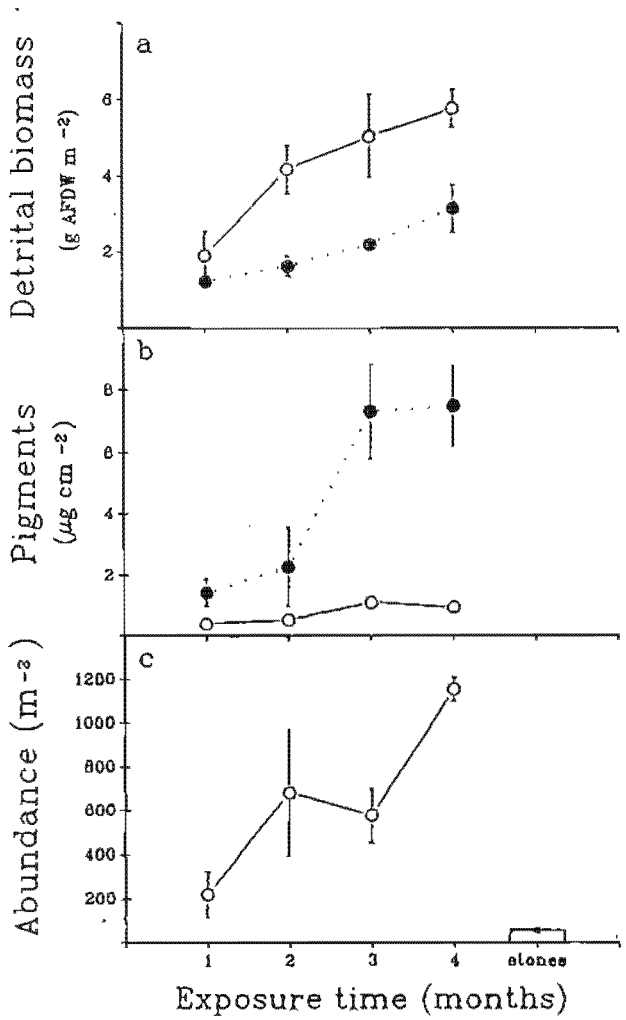


Fig. 9a: Quantities of trapped detritus in stone-filled baskets exposed for 1, 2, 3 and 4 months at Mouse Stream (x ± 1 SE, n=5). Open bars = CPOM; striped bars = FPOM.

Fig 9b: Concentrations of chlorophyll *a* and phaeopigments extracted from algae colonizing stones in baskets exposed for 1, 2, 3 and 4 months at Mouse Stream (x ± 1 SE, n=5). Open bars = chlorophyll *a*; striped bars = phaeopigments.

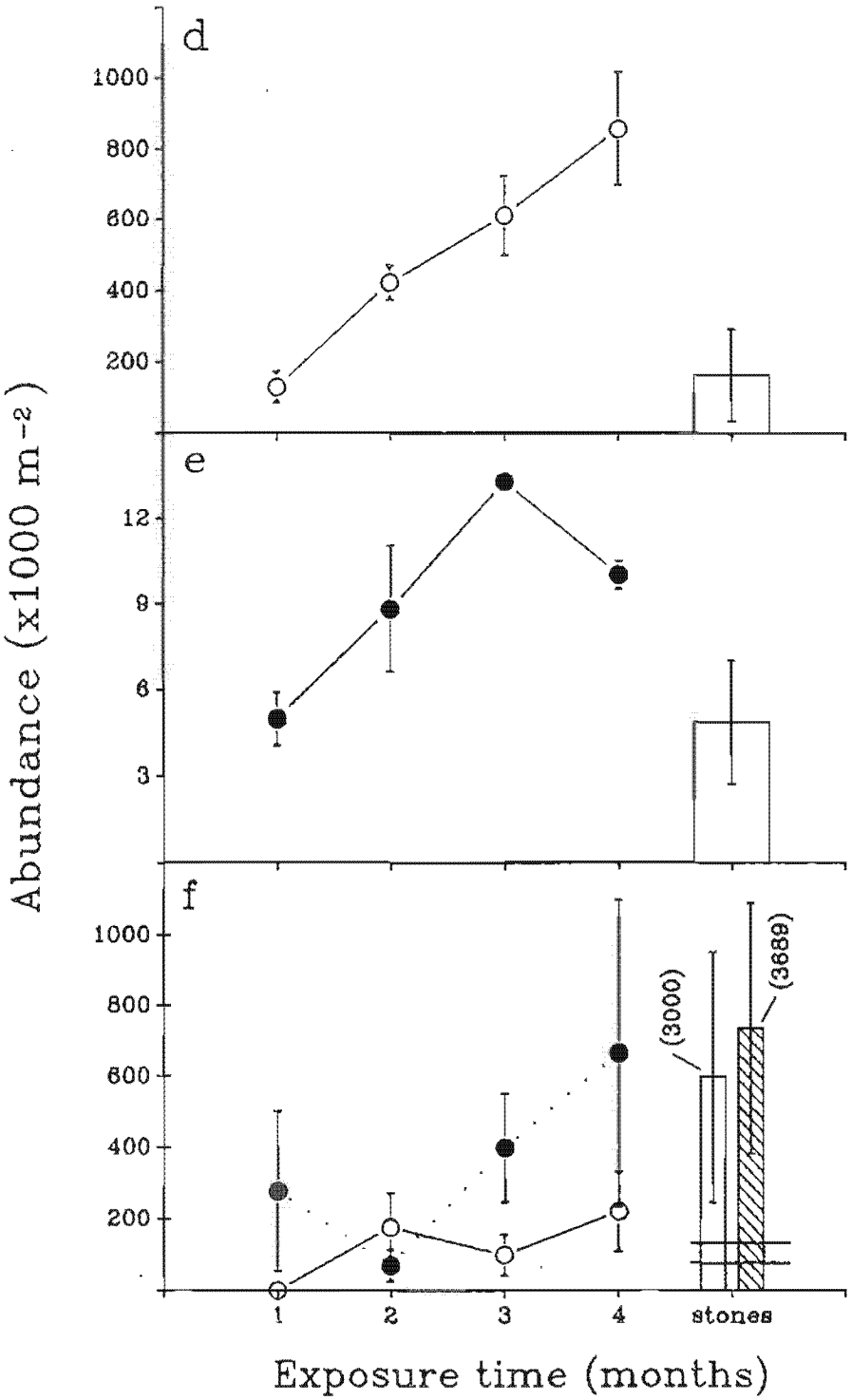
Figs 9c-f: Densities of invertebrates colonizing stone-filled baskets set out for 1, 2, 3 and 4 months at Mouse Stream (x ± 1 SE, n=5).

c: density of pupating chironomids.

d: density of chironomid larvae.

e: density of *Deleatidium* larvae.

f: densities of nematodes (open circles and bar) and ostracods (closed circles and striped bars).


d
e
f
1000
800
600
400
200
12
9
6
3
(3000)
(3689)
1
2
3
4
stones
Abundance (x1000 m-2)
Exposure time (months)

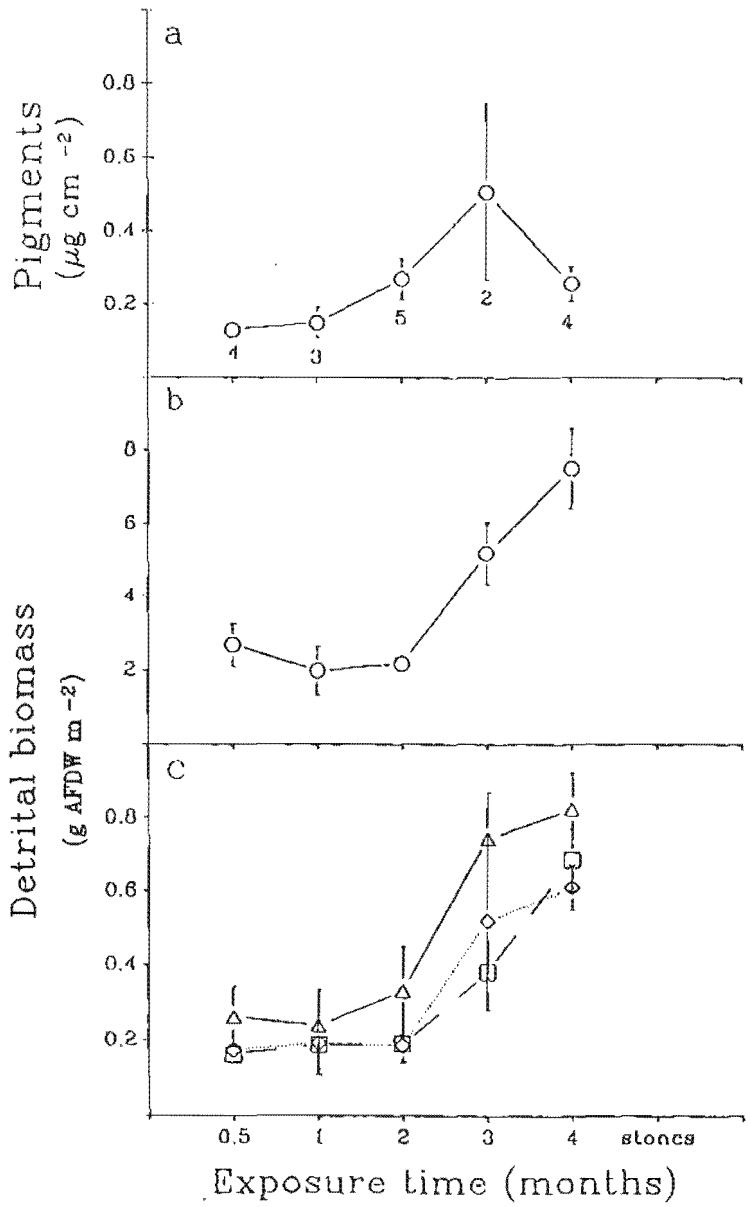
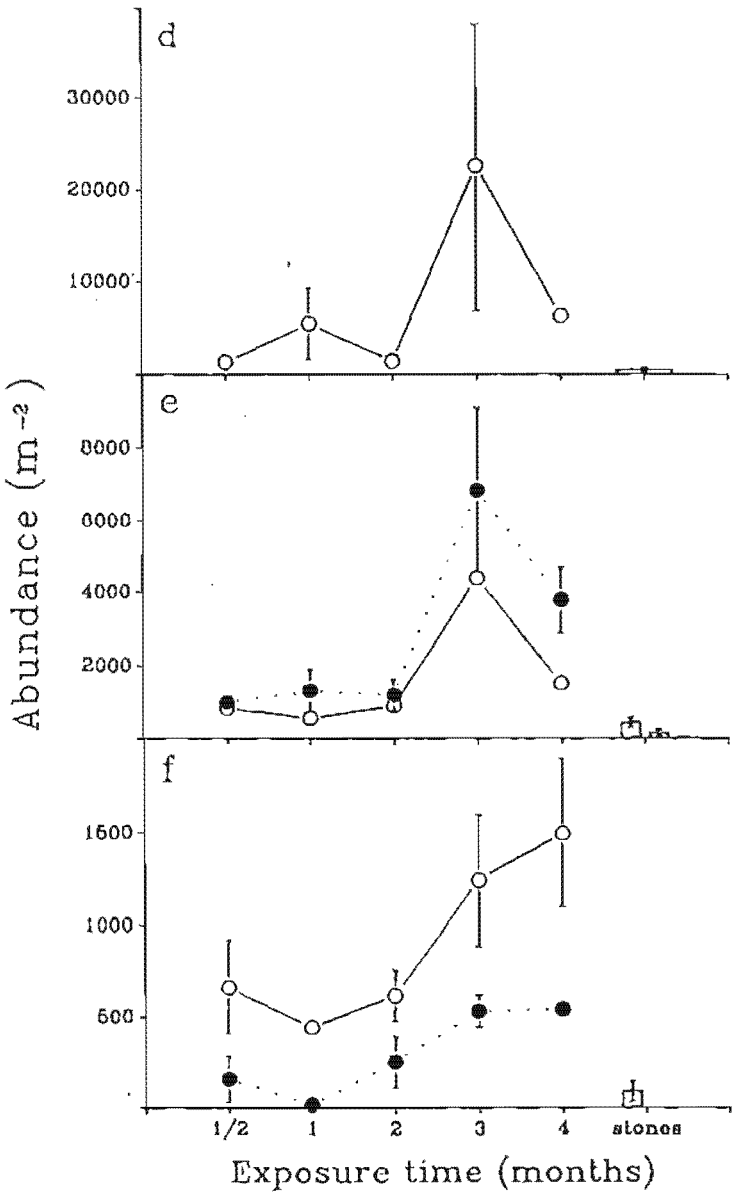


Fig. 10a: Concentrations of chlorophyll *a* extracted from algae colonizing stones in baskets exposed for 0.5 1, 2, 3 and 4 months at Tim's Creek (x ± 1 SE, n is represented by the numbers below each point.)

Figs 10b-c: Quantities of detritus trapped in stone-filled baskets exposed for 0.5 1, 2, 3 and 4 months at Tim's Creek (x ± 1 SE, n as Fig 9a). Open circles (Fig. 9b) = LPOM; opened triangles = CPOM; open squares = MPOM; open diamonds = FPOM (Fig 9c).



Figs **10d-f:** Densities of invertebrates colonizing stone-filled baskets set out for 1, 2, 3 and 4 months at Tim's Creek ($\bar{x} \pm 1$ SE, n as in Fig 10a).

d: density of chironomid larvae.

e: density of *Deleatidium* larvae (open circles and bar) and copepods (closed circles and striped bar).

f: densities of *Zelandobius* larvae (open circles and bar) and *Spaniocera zelandica* larvae (closed circles).

Of the 33 riffle dwelling taxa analysed, only 8 showed habitat preferences as determined by ANOVA. Densities of *Zelandobius*, and *S. zelandica* were highest in the longest exposed substrata, whereas densities of chironomid larvae, *Deleatidium*, copepods, and an oribatid mite were highest in substrata incubated for 3 months ($F= 4.02, 9.35, 3.71, 5.40, 3.65, 5.02$, respectively, $p<0.01$). Densities of all these taxa were lower in unenclosed natural riffles than baskets (Figs 10 d,e,f). Densities of the mite *Zelandobatella naias* and larval Ceratopogonidae varied independently between stony baskets and natural riffles.

Densities of only 8 taxa were significantly correlated with the measured environmental variables. Phaeopigment content was positively correlated with most taxa (5), whereas CPOM and time were correlated with 1 taxon each (Table 3).

MPOM and CPOM were the most powerful predictor variables, explaining over 80% of the variation in densities of *S. zelandica* and an oribatid mite (Table 4c). MPOM also explained 66% of the variation in taxonomic richness in stony baskets. Over 50% of the variation in densities of copepods, chironomids, *Deleatidium* and total invertebrates was explained by phaeopigment concentrations (Table 4c).

Calculated regression models for individual taxa had high predictive powers, and explained over 80% of the variation in total invertebrate densities and densities of the stonefly *S. zelandica*, the tipulid *Paralimnophila skusei* Hutton and an oribatid mite (Table 4c).

(iv) Importance of algae and detritus

MOUSE STREAM

Use of Vydate to remove animals on artificial substrates allowed invertebrate colonization patterns to be compared between freshly placed substrates without significant algal and detrital biomass, and preconditioned structures with significant algal and detrital biomass.

Substrates in the first experiment at Mouse Stream were exposed for one and four months. Biomass of algae (as indicated by chlorophyll *a* and phaeopigment concentration) and trapped detritus, and invertebrate densities were not significantly different between the control substrates (exposed for 4 months) and either the Vydate treated preconditioned structures or the newly placed structures exposed for one month ($F= 0.24, 1.88$ for chlorophyll *a* and phaeopigment; $F= 1.01, 1.42, 0.79, 0.76$ for LPOM, CPOM, MPOM, FPOM; $F= 1.68$ for total abundance; $p>0.05$). Thus, organic matter accumulation and invertebrate colonization of the newly placed structures was rapid, and increased to levels similar to those found on the structures exposed in the stream for 4 months. As the organic matter biomass and invertebrate densities did not increase between one and four months, it seems likely that the carrying capacity of these substrates was reached within one month and did not

Table 5: Invertebrate abundance, taxonomic richness, and biomass of FPOM and algal pigments on artificial bryophytes exposed for different lengths of time in Mouse Stream ($\bar{x} \pm$ 1SE, n = 5). Some substrates were treated with the insecticide/nematicide Vydate after 3 weeks so that rates of invertebrate colonization could be compared after a 1 week exposure with and without substantial algal and detrital biomass present. Asterisk denotes those variables which were not significantly different from each other (Tukey's test; $p < 0.05$).

VARIABLE	EXPOSURE TIME		
	1 week	4 weeks	4 weeks (Vydate treated)
FPOM (g AFDW m^{-2})	4.06 ± 0.61	7.26 ± 0.55 (*)	5.50 ± 0.73 (*)
chlorophyll *a* ($\mu g\ cm^{-2}$)	2.97 ± 0.59	8.90 ± 1.07 (*)	7.28 ± 1.30 (*)
phaeopigments ($\mu g\ cm^{-2}$)	2.54 ± 0.66	10.09 ± 1.95 (*)	9.81 ± 1.65 (*)
invertebrate abundance (m^{-2})	66 660 ± 6981	304 000 ± 43 980 (*)	168 200 ± 13 240 (*)
taxonomic richness (m^{-2})	13.8 ± 1.2	18.4 ± 1.5 (*)	15.8 ± 0.7 (*)
Muscidae sp. A (m^{-2})	25 ± 5	76 ± 23 (*)	57 ± 15 (*)
Chironomidae - larvae (m^{-2})	43 600 ± 5753	216 400 ± 39620 (*)	112 900 ± 11 490 (*)
Acroperla spiniger (m^{-2})	40 ± 25	280 ± 92 (*)	180 ± 49 (*)
Tardigrada (m^{-2})	1460 ± 575	6560 ± 1489 (*)	4800 ± 1859 (*)
Copepoda (m^{-2})	10 090 ± 3419	59 480 ± 8034 (*)	35 840 ± 6895 (*)
Hydrobiosis silvicola (m^{-2})	20 ± 20 (*)	160 ± 68	20 ± 20 (*)
Chironomidae - pupae (m^{-2})	20 ± 20 (*)	340 ± 144	20 ± 20 (*)

Table 6: Invertebrate abundance, and biomass of MPOM, FPOM and algal pigments on artificial bryophytes exposed for different lengths of time in Tim's Creek ($x \pm$ 1SE, n = 5). Some substrates were treated with the insecticide/nematicide Vydate after 3 weeks so that rates of invertebrate colonization could be compared after a 1 week exposure with and without substantial algal and detrital biomass present. Asterisk denotes those variables which were not significantly different from each other (Tukey's test: $p < 0.05$).

	EXPOSURE TIME		
VARIABLE	1 week	4 weeks	4 weeks + Vydate
MPOM ($x10^{-2}$g AFDW m^{-2})	4.24 ± 0.37	6.74 ± 0.67 (*)	5.64 ± 0.63 (*)
FPOM ($x10^{-2}$g AFDW m^{-2})	5.72 ± 4.97	10.12 ± 1.45 (*)	9.02 ± 1.25 (*)
chlorophyll *a* (μg cm^{-2})	0.36 ± 0.03	0.715 ± 0.07 (*)	0.67 ± 0.04 (*)
phaeopigments (μg cm^{-2})	0.24 ± 0.03	0.35 ± 0.02 (*)	0.35 ± 0.04 (*)
Spaniocerca zelandica (m^{-2})	40 ± 25	240 ± 75 (*)	125 ± 48 (*)
Empididae sp. B (m^{-2})	1220 ± 361	2380 ± 483 (*)	3475 ± 823 (*)

increase with longer exposure time.

In the second experiment FPOM biomass, and concentrations of chlorophyll *a* and phaeopigment were significantly lower on artificial bryophytes exposed for 1 week than on those exposed continuously for 4 weeks or treated with Vydate after 3 weeks (F= 6.35, FPOM; F= 8.81, 7.94 chlorophyll *a* and phaeopigment respectively, $p<0.01$; Table 5).

Total invertebrate abundance and taxonomic richness were also lower on artificial bryophytes exposed for 1 week than either the control or preconditioned substrata (F= 47.36, total abundance; F= 3.86, taxonomic richness, $p<0.01$, Table 5). Densities of 7 taxa differed significantly between artificial substrata exposed for 1 week and substrata treated with Vydate. Thus, densities of larval muscids and chironomids, the stonefly *A. spiniger*, tardigrades and copepods (Table 5) were higher on the Vydate treated substrata than on untreated substrata exposed for 1 week. Larvae of the caddisfly, *Hydroblosis silvicola*, and pupating chironomids (Table 5) were the only animals which colonised both Vydate treated and 1 week exposed substrata less than those exposed for 4 weeks.

TIM'S CREEK

Artificial bryophytes

No differences existed between quantities of LPOM and CPOM trapped by the preconditioned artificial bryophytes or those exposed for 1 week (F= 1.77, 2.75 respectively, $p>0.05$). However, artificial bryophytes exposed for 1 week contained significantly less MPOM, FPOM and algae (chlorophyll *a* and phaeopigment concentrations) than both the preconditioned and control substrates which were exposed for 4 weeks (F= 4.79, 4.06, for MPOM and FPOM; F= 15.9 and 5.48 for chlorophyll *a* and phaeophytin respectively, $p<0.05$; Table 6).

Although total invertebrate density was lower on artificial bryophytes set out for 1 week, densities were not significantly different between substrata (F= 1.94, $p>0.05$). Of the 16 taxa analysed, only *S. zelandica* and an empidid were less abundant on artificial bryophytes exposed for 1 than 4 weeks (both control and Vydate treated samples) (F= 3.80, 4.05 respectively, $p<0.05$; Table 6). Densities of all other 14 taxa on experimental substrata were independent of both detrital biomass (MPOM, FPOM) and periphytic algal standing crop.

Stone baskets

The newly placed stone filled baskets exposed for 2 weeks trapped significantly less organic matter of all size fractions than the control baskets, placed in the stream 3.5 months previously. Both newly placed baskets and those treated with Vydate however contained similar quantities of detritus (F= 10.21, 10.57, 14.78 10.00 for LPOM, CPOM, MPOM, and FPOM, $p<0.01$; Table 7). Although some baskets

Table 7: Invertebrate abundance, taxonomic richness, and biomass of trapped detritus in stone-filled baskets exposed for different lengths of time in Tim's Creek ($x \pm 1SE$, n as in Fig.9). Some substrates were treated with the insecticide/nematicide Vydate after 3.5 months so that rates of invertebrate colonization could be compared after a 0.5 month exposure with and without substantial algal and detrital biomass present. Asterisk denotes those variables which were not significantly different from each other (Tukey's test; $p < 0.05$).

	EXPOSURE TIME		
VARIABLE	0.5 month	4 month	4 month + Vydate
LPOM (g AFDW m^{-2})	2.69 ± 0.58 (*)	7.51 ± 1.09	3.66 ± 0.51 (*)
CPOM (g AFDW m^{-2})	0.26 ± 0.08 (*)	0.83 ± 0.09	0.49 ± 0.10 (*)
MPOM (g AFDW m^{-2})	0.16 ± 0.03 (*)	0.69 ± 0.09	0.34 ± 0.09 (*)
FPOM (g AFDW m^{-2})	0.18 ± 0.03 (*)	0.61 ± 0.09	0.31 ± 0.14 (*)
Invert abundance (m^{-2})	6244 ± 1934	24 233 ± 3064 (*)	13 940 ± 2595 (*)
taxonomic richness (m^{-2})	16 ± 2.0	23.8 ± 0.5 (*)	20.0 ± 1.5 (*)
Chironomidae - larvae (m^{-2})	1344 ± 783	6322 ± 1109	3081 ± 1186
Stenoperla prasina (m^{-2})	156 ± 127 (*)	544 ± 58	193 ± 65 (*)
Zelandobatella naias (m^{-2})	0	978 ± 638 (*)	711 ± 205 (*)
Oribatidae sp. A (m^{-2})	44 ± 44 (*)	756 ± 89	59 ± 59 (*)
Ceratopogonidae (m^{-2})	0 (*)	200 ± 69	0 (*)

lost a little organic matter during the Vydate treatment, they would still have contained more detritus upon replacement than the newly placed baskets. The similar quantities of detritus trapped in baskets exposed for 2 weeks and baskets exposed for 4 months and treated with Vydate indicates that litter inputs into the newly placed baskets were high.

Algal colonization of newly placed baskets was also rapid, and no difference in pigment concentrations was found on stones in baskets exposed for 2 weeks and on stones in baskets exposed for 4 months (both control and Vydate treated; $F= 3.27, 1.64$, $p>0.05$).

However, total invertebrate abundance and taxonomic richness were highest in baskets exposed for 4 months, and lowest in baskets exposed for 2 weeks ($F= 12.03, 6.90$; $p<0.01$; Table 7). Invertebrate density and taxonomic richness were intermediate on Vydate treated samples, suggesting there had been slightly more rapid recolonisation of these substrata than of newly placed baskets.

Densities of only five of the 24 taxa analysed differed among treatments. Larval chironomids, the stonefly *S. prasina* (Newman) and two mites, *Zelandobatella naias* and an oribatid, colonised the 2 week exposed baskets poorly, and baskets placed out 3.5 months previously, best ($F= 4.96, 6.66, 9.12, 6.21$ respectively, $p<0.05$; Table 7). Baskets exposed for 4 months contained more ceratopogonid larvae than either the 2 week or Vydate treated baskets ($F= 102.9$; $p<0.001$; Table 7).

DISCUSSION

Algal biomass (as measured by chlorophyll *a* and phaeopigment) increased on artificial bryophyte substrata to a maximum after 4 weeks in both streams. Similar results were obtained by Biggs (1988) in larger rivers with low nutrient concentrations, where algal biomass peaked after 4 weeks and then usually declined. He attributed this to sloughing of older algae, but I did not observe this in my study.

Current velocity has been implicated as an environmental factor regulating quantities of periphyton in streams (Traaen & Lindstrom 1983, Reiter & Carlson 1986, Biggs & Close 1989), but periphyton biomass on mosses exposed for 8 weeks at both sites did not decrease when stem density (i.e., shelter) was reduced. This may have reflected a reduction in self-shading in low "stem" density substrata, and more intimate associations between algal cells and the surrounding water which may have enabled greater cellular uptake of nutrients. Phaeopigment concentration also did not change with decreasing "stem" density, but concentrations of this pigment increased markedly over time on full density mimics at both sites. This indicates that the latter communities (up to 4 weeks old) were at a more advanced stage of senescence than communities associated with low density mosses (up to 8 weeks old) possibly because of reduced light or nutrients, as discussed above.

Periphyton colonisation rates and biomass were greater on artificial bryophytes than on stones held in baskets. Thus, chlorophyll *a* concentrations were 2 and 7 times greater on artificial bryophytes than stones at Tim's Creek and Mouse Stream respectively after 4 weeks. The artificial bryophyte analogues provided algal colonizers with a stable substrate in areas of high water velocity, whereas stones in riffles (and baskets) were constantly being disturbed. The very high phaeopigment concentrations associated with stones in baskets at Mouse Stream (79% after 1 month, 89% after 4 months) may also reflect continual destruction of older algal communities exposed to harsh physical conditions.

Algal biomass was considerably higher on artificial bryophytes and stones above the tree-line than within the beech forest. Chlorophyll *a* and phaeopigment concentrations on artificial bryophytes at Mouse Stream were respectively 10 and 17 times greater than at Tim's Creek after 4 weeks, and concentrations of these pigments extracted from algae present in the stone-filled baskets were 3 and 51 times higher at Mouse Stream than Tim's Creek after 4 weeks. Although higher light intensity above the tree-line is probably the primary reason for this enhancement, increased habitat stability at Mouse Stream appears to have also enhanced algal development.

The accumulation of detritus by experimental substrata was not strongly time dependent and was probably determined by a combination of input rates and hydrologic conditions. Nevertheless, the amount of detritus trapped in baskets at both sites, and by artificial bryophytes at Mouse Stream increased with time up to 1 month.

At Mouse Stream, artificial bryophytes set out for 1-4 months trapped more organic matter than stone-filled baskets, whereas the reverse was true at Tim's Creek. While apparently contradictory, this appears to reflect differences in quantities of allochthonous inputs at each site and differences in substrate stability.

Allochthonous inputs to Mouse Stream were lower than to Tim's Creek (Chapters 2 & 7), yet flow regime and channel gradient were less at the former. Thus, litter entering Mouse Stream could be trapped more easily by bryophytes, artificial bryophytes, or stones in riffles. However, the presence of litter appeared to be more transient in riffles. At Tim's Creek, riffles were also unstable and stone-filled baskets provided exceptionally stable microhabitats that accumulated more detritus than Surber samples taken from adjacent, unenclosed sites.

The experimental protocol used essentially examined invertebrate colonisation dynamics on different substrata. Colonization is a multifaceted sequence of events that depends upon substratum nature (McAuliffe 1983, Doeg *et al.* 1989), the type of stream fauna and season (Benson & Pearson 1987) and the source of incoming colonists. Although colonization has been likened to molecular diffusion, whereby invertebrates move from high to low density areas (Sheldon 1984), it is not as simple as that. The presence of periphyton and trapped FPOM on substrata often profoundly influence behaviours of colonizing invertebrates (Roby *et al.* 1978, Boothroyd & Dickie

1989), and some grazing invertebrates actively track periphyton abundance and selectively colonize areas rich in this food (McAuliffe 1983).

Although I found that invertebrates responded to changes in substrate quality (i.e., algal and detrital biomass) in all experimental manipulations, the numerical response of each taxon varied between sites and between substrata. At Mouse Stream, invertebrate densities attained on artificial bryophytes and in baskets were generally highest where organic matter biomass, algae biomass, or shelter were greatest.

Colonization patterns at Tim's Creek however, were inconsistent and only poor relationships were evident between invertebrate density and quantities of algae, trapped detritus and shelter. In fact, positive relationships with periphyton or detrital biomass were evident for only three of 22 invertebrate taxa associated with artificial bryophytes (weekly experimental series), and only seven of 35 taxa associated with stone baskets. This lack of a strong patch selection by invertebrates at Tim's Creek is likely to reflect the occurrence of more spates and its higher streambed instability. Colonization processes here are thus expected to be influenced more by stochastic events than biotic interactions (Townsend 1989), and is consistent with the scenario advanced by Peckarsky (1983) whereby biotic interactions (e.g., the tracking of areas high in periphyton or detrital biomass) in "harsh" environments (i.e., Tim's Creek) are masked by chance abiotic interactions.

Aquatic bryophytes are generally considered to serve primarily as shelter for invertebrates (Glime & Clemons 1972) and indeed Percival & Whitehead (1929) found that thick moss mats supported more invertebrates than thin mats. Plant morphology, and by inference shelter, has often been implicated as influencing invertebrate abundances on plants (e.g., Krecker 1939, Rooke 1984, 1986a,b, Cyr & Downing 1988), and I anticipated that the reduced stem density artificial bryophytes would be colonised by fewer invertebrates than full density substrata. This was evident at Mouse Stream where total invertebrate abundance, taxonomic richness and the densities of five of nine common taxa were negatively affected by reductions in stem density. However, at Tim's Creek, reductions in stem density affected only two taxa. Quantities of algae and detritus at both sites were unaffected by decreases in stem density, so it seems unlikely that reduced invertebrate abundances were a result of food limitation. Rather it is likely that more shelter was available to colonists when stem density was higher, and that this was more important to them at Mouse Stream than Tim's Creek.

Although stem density influenced colonisation of some invertebrates, quantities of algae and detritus also strongly affected invertebrate distributions. In my experiments with Vydate, treated mimics already colonized by periphyton and containing detritus attracted more invertebrates than uncolonised substrata set out in Mouse Stream for the same period of time. This suggests that invertebrates actively cued into patches of dense periphyton, as has been described elsewhere by McAuliffe (1983), Olgivie & Clifford (1986) and Winterbourn (1990).

In contrast to the results obtained at Mouse Stream, invertebrate recolonisation of Vydate treated substrata at Tim's Creek appeared to be independent of algal and detrital biomass. This again may reflect the more stochastic nature of this site where biotic interactions are unimportant, and may also be a consequence of the different colonizing abilities of taxa at Tim's Creek. Thus it appears that the influence of algae and detritus can be both taxon and site specific.

The relationships between invertebrate densities and measured environmental variables was examined by stepwise regression analysis. In Mouse Stream, highly significant regressions were obtained between abundances of some invertebrates and quantities of either CPOM, MPOM, and FPOM, chlorophyll *a* or phaeopigments present on artificial bryophytes exposed for 1 to 4 weeks. In particular, colonisation of artificial bryophytes by *A. spiniger, Zelandobius, L. hudsoni,* Chironomidae and Copepoda appeared to be strongly influenced by the amounts of trapped detritus as well as algal biomass, whereas shelter (i.e., stem density) was also an important predictor variable for the stonefly *Zelandobius.* Invertebrate densities in stone-filled baskets were also correlated with detrital biomass, but no riffle dwelling taxon showed a density relationship with algal biomass.

At Tim's Creek, densities of most invertebrates colonizing artificial bryophytes were not correlated with quantities of trapped detritus or algae, again illustrating the importance of stochastic events in regulating invertebrate colonization patterns and making invertebrate colonisation independent of these variables. However, strong relationships were obtained between the abundances of chironomids, nematodes and empidids, and quantities of detritus and algae associated with reduced stem density artificial bryophytes. These structures all contained less detritus and algae than full density artificial bryophytes, and consequently this material may have limited invertebrate colonisation of substrata offering reduced shelter. In contrast, invertebrates colonizing stone-filled baskets at Tim's Creek showed strong numerical responses to detrital biomass (CPOM and MPOM) and algal standing crop. The strong associations between detritus trapped in stone baskets is not surprising, considering its enhanced retention here. The influence of algae in affecting total invertebrate numbers, and densities of chironomids, *Deleatidium* and copepods, was surprising considering the low algal biomass at this site, but presumably reflects a food relationship.

CONCLUSIONS

Colonization patterns of invertebrates and their relationships with associated environmental factors differed at the two experimental sites. At Mouse Stream, where algal biomass and substrate stability were high, many invertebrates responded to enhanced detrital and algal biomass with which their densities were positively correlated. Invertebrate densities stabilized after about 1 month. Invertebrate densities

were also positively related to the amount of shelter provided by the artificial bryophytes as assessed by their number of "stems".

At Tim's Creek, however, the stream bed was generally less stable, discharge was more variable and both algal biomass and retention of allochthonous litter inputs was lower. Invertebrate densities at Tim's Creek showed weak relationships with the biomass of organic matter trapped by full density artificial bryophytes, either because increased habitat instability masked such relationships or because the quantities of detritus trapped were in excess of invertebrate requirements. However, a clear relationship between invertebrate density and trapped MPOM and FPOM was observed in reduced density artificial bryophytes, which may indicate either a food, or shelter related relationship.

Riffle dwelling invertebrates also responded positively to CPOM, MPOM and FPOM biomass in both streams. Senescent algal tissue (as indicated by phaeopigment values) was associated with high densities of animals at Tim's Creek, suggesting that the presence of decomposing algal material may influence invertebrate densities.

Although many New Zealand mountain streams have poor retention characteristics (Winterbourn 1986, Graesser 1988), it is clear that the densities of benthic invertebrates in both riffles and bryophytes is sometimes related to the distribution of trapped organic matter. This was also found in a sub-alpine stream at Cass, 30 km. east of Tim's Creek where significant correlations between the densities of some benthic species and quantities of CPOM and FPOM were observed (Winterbourn 1978, Winterbourn 1982b).

Artificial bryophytes, like living bryophytes, reduce currents within their matrices and provide a depositional area for organic materials and a stable substrate for periphyton colonisation. Some invertebrates associated with artificial bryophytes increase in abundance with increases in trapped organic material or algae, and might be expected to similarly colonise living bryophytes. Although a few taxa colonise living bryophytes to consume them (e.g., Byers 1961, Willoughby & Mappin 1988), my results indicate that colonisation by most invertebrates was independent of the value of the plant as a food source. Instead it depended on the biomass of algae and organic matter trapped by them, and the degree of shelter they provide.

CHAPTER SIX:

CONSUMPTION OF AQUATIC BRYOPHYTES BY ALPINE STREAM INVERTEBRATES AND THEIR FOOD VALUE

INTRODUCTION

Aquatic bryophytes often proliferate on stable boulders and bedrock in New Zealand alpine streams, and can support high densities of invertebrates, both here (Chapter 2) and elsewhere (Percival & Whitehead 1929, Hynes 1961, Glime 1968, McElhone & Davies 1985, McKenzie-Smith 1987). Discrete invertebrate communities are frequently associated with these plants, and in New Zealand many taxa (e.g., Chironomidae, *Zelolessica cheira, Limonia hudsoni, Zelandoperla* spp., Nematoda and Tardigrada) preferentially colonize them rather than stony riffles.

Although numerous reports document aquatic bryophyte herbivory (e.g., Alexander 1920, Brindle 1959, Bryce 1959, Byers 1961, Erichsen-Jones 1969, Gerson 1972, Fuller & Stewart 1977, Williams & Williams 1982, Mutch & Prichard 1984a, b, Willoughby & Mappin 1988, Wyatt & Stoneburner 1989), consumption generally appears to be limited, and less than expected (Frankland 1974, Gerson 1982, Lawrey 1987), especially when the wide diversity of bryophyte dwelling invertebrates is considered.

Frequently associated with aquatic bryophytes are large quantities of periphyton (Douglas 1958, Johnson 1978, Maurer & Brusven 1983, Suren 1988). Many invertebrates have been shown to actively colonize areas with high periphyton biomass (McAuliffe 1984) and in some instances reduce standing crops by intensive grazing (Jacoby 1985, 1987, Hill & Knight 1987, Feminella *et al.* 1989). Invertebrate colonization of mosses may thus reflect the abundant presence of an algal food source. Similarly, detritus that accumulates amongst entwined stems at the bases of bryophytes (Lindegaard *et al.* 1975, Devantry 1987, Smith-Cuffney 1987) may attract invertebrates to these environments.

In this chapter I consider the food and feeding behaviour of selected invertebrates found associated with bryophytes in two New Zealand alpine streams. Gut contents of a wide range of animals collected from bryophyte habitats were examined for evidence of bryophagy. Because ingestion does not equate with assimilation, stable carbon isotope analysis was conducted on a number of taxa that were found to consume bryophytes. This was done to determine whether bryophyte carbon is actually incorporated into body tissues, or whether ingestion is "accidental", i.e., a consequence of grazing periphyton or accumulated detritus that is often intimately associated with bryophytes.

As bryophyte consumption may be related to plant food quality, the crude biochemical composition of various bryophyte taxa was also examined and compared with that of surrounding riparian vegetation, both fresh and following a 2-month conditioning period.

MATERIALS AND METHODS

Gut content analysis

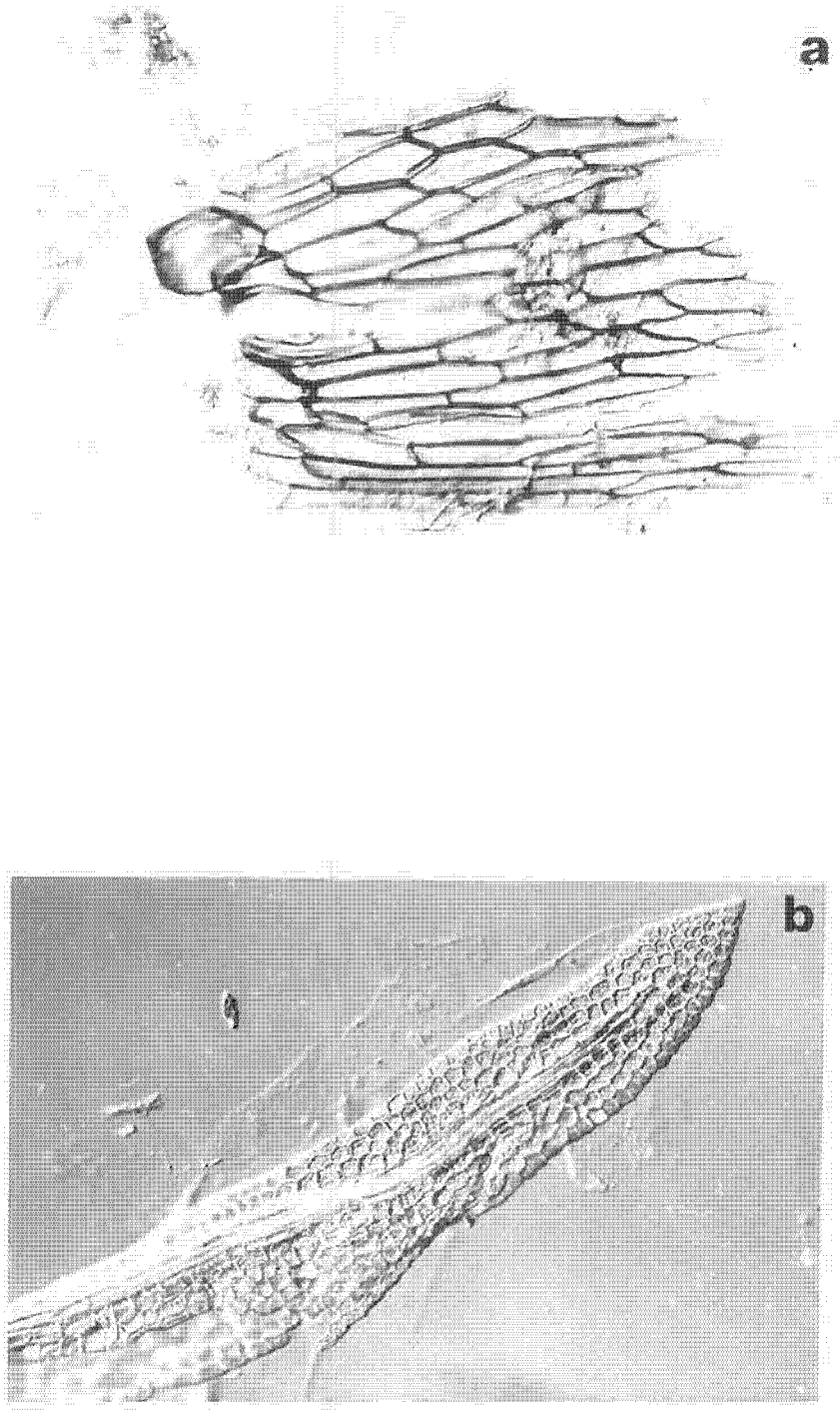
Bryophytes support distinct invertebrate assemblages, often at high densities (Chapter 2). To determine how widespread bryophagy is amongst these animals, I examined the guts of as many taxa as possible for presence of bryophyte fragments. Following this, I made quantitative observations on gut contents of selected taxa to determine the percentage occurrence of bryophytes and other food items ingested by invertebrates in the two sites.

All animals collected in my initial 18 month survey (Chapter 2) were frozen (-18°C) immediately after sorting. For gut analysis, selected animals were thawed and placed in a drop of water on a coverslip. Entire guts were removed and their contents were teased apart with fine forceps. Following evaporation of most of the water on the coverslip, the gut contents were thoroughly mixed with a drop of lactophenol-PVA. Gut contents of small animals (e.g., early instars of Chironomidae, *Zelolessica cheira*, *Orchymontia dispersa* *Zelandoperla* spp., *Zelandoblus* spp., *Cristaperla fimbria*) were pooled in groups of up to 5 individuals.

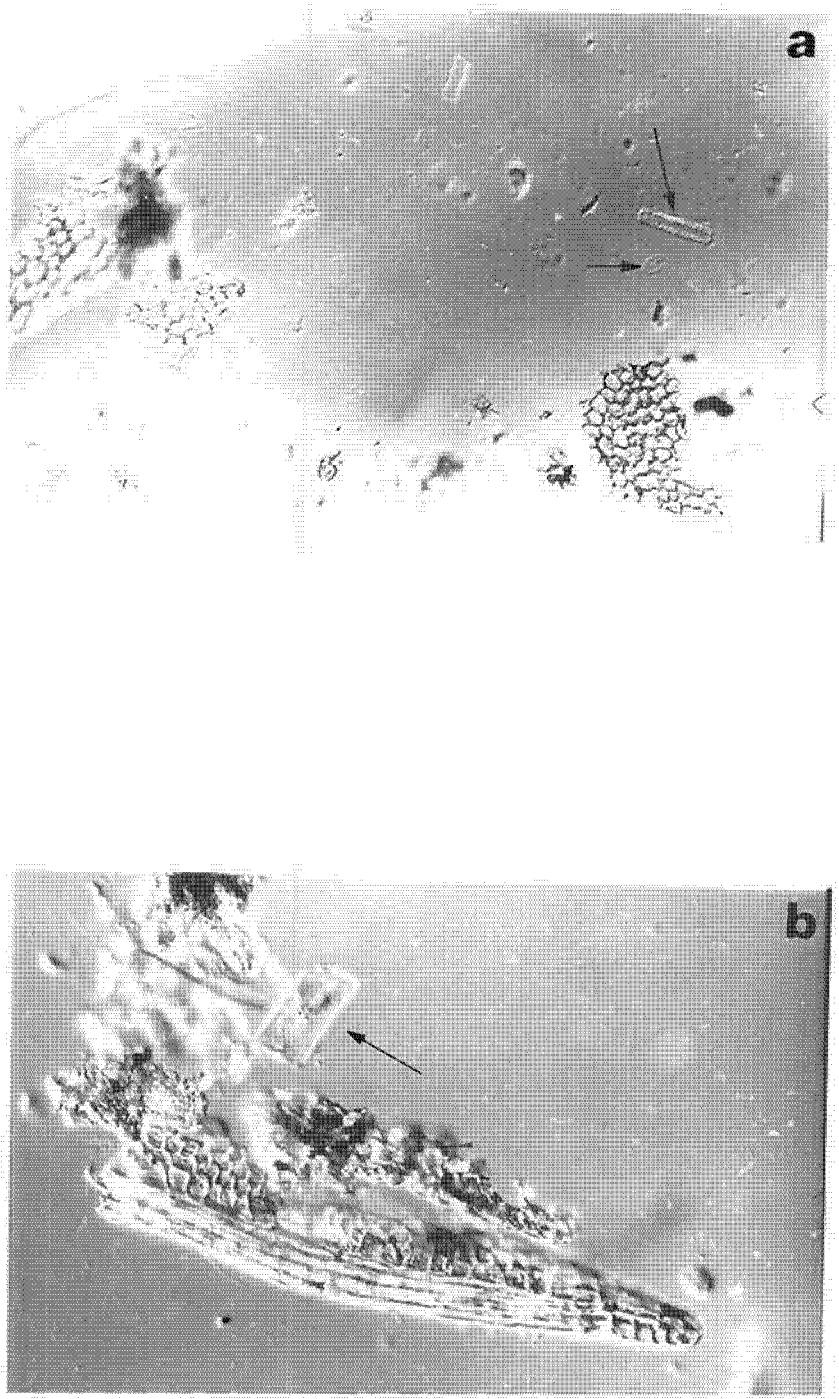
Following air drying, slides were examined with a phase contrast microscope (Olympus BH-2) at x200 magnification. Ten fields of view were selected at random and the frequency of individual food items within a gridded eyepiece (100 squares) was recorded. Food items were placed in 6 major categories: bryophytes (Figs 1a,b), algae (Figs 2a,b), fungi (Figs 3a,b), animal remains (Fig. 4), riparian vegetation and detritus. Each of these was subdivided into more discrete categories where possible (Table 1). Detritus consisted of any material without recognizable cellular structure (e.g., Fig. 5), and was divided into 3 size categories. If cellular detail was recognizable, and it was not of bryophyte origin, then the material was deemed to be from vascular plants. The degree of observed "conditioning" of this material by microbes was qualitatively assessed to determine whether the material was fresh or not (e.g., Figs 6 & 7) depending upon quantities of fungi present and the physical appearance of cells.

Stable carbon isotope analysis

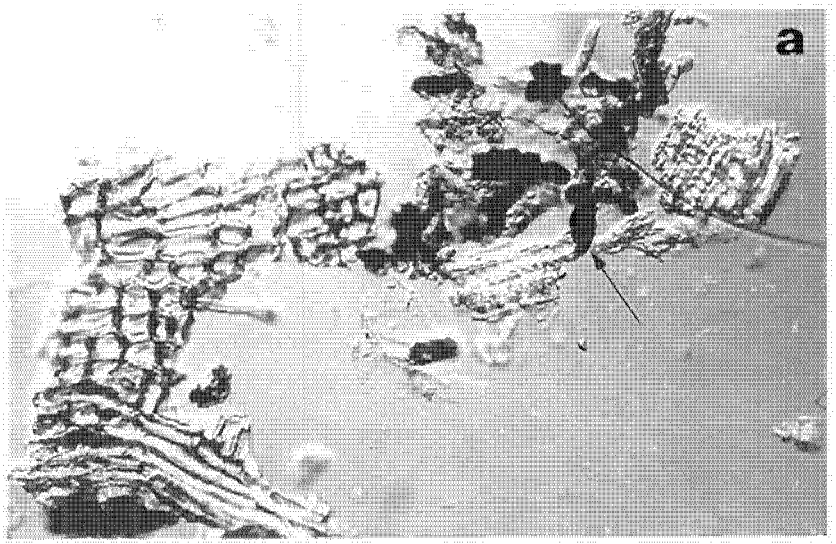
Gut content analyses were supplemented with stable carbon isotope analyses which can provide information on the long-term nature of food resources utilized by animals as their $^{13}C/^{12}C$ ratio should reflect that of their food (Rounick & Winterbourn 1986, Winterbourn *et al.* 1986). The technique depends on different food materials having contrasting stable carbon isotope ratios. This is not always the case, but as aquatic mosses utilize dissolved atmospheric CO_2 for photosynthesis (Bain & Proctor 1980, Glime & Vitt 1984, Maberly 1985a,b), they are likely to have ratios distinct from those of many algae and terrestrial plants. To test for isotopic differences in potential food source, samples of bryophytes, riparian plant species and algae were collected from each site and transported to Christchurch on ice. Riparian vegetation was taken from living

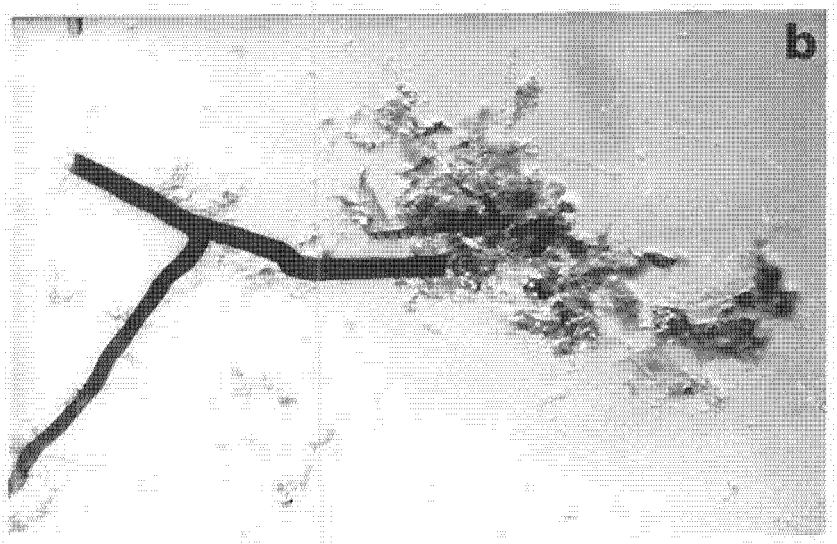


Figs 1: Bryophyte material in the guts of *Limonia hudsoni* larvae. a = basal portion of *Bryum blandum* leaf (x200), b = upper portion of *Fissidens rigidulus* leaf (x100).



Figs 2: Gut contents of *Limonia hudsoni* larva showing periphytic algae, (arrowed), usually associated with bryophytes. a = *Diatoma* and *Navicula* in the presence of mid-leaf fragments of *Fissides rigidulus* (x200); b = *Tabellaria* and leaf margin of *F. rigidulus* (x200).





Figs 3: Gut contents of *Austroperla cyrene* larvae. a = sooty mould fungus (arrowed) in association with the basal portion of a *F. rigidulus* leaf (x200); b,= a branched septate fungal hypha and fine detrital material (x200).

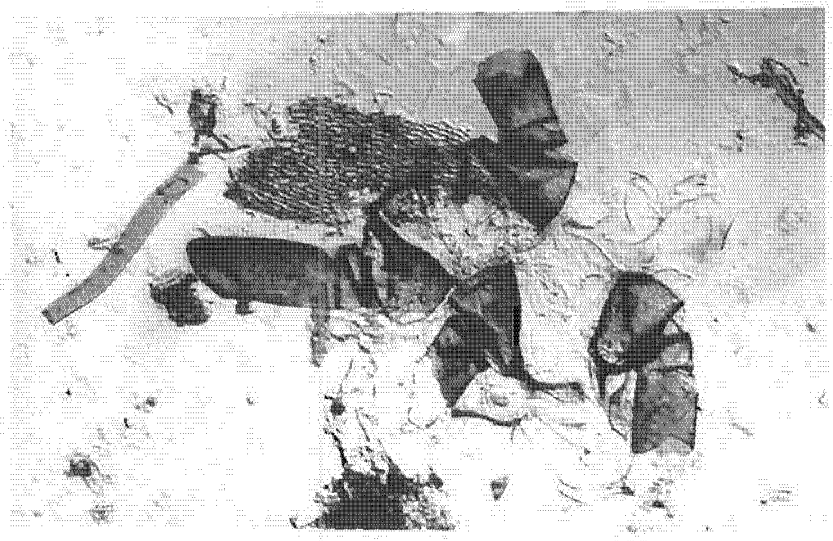


Fig.4: Remains of an unidentified stonefly larva (probably *Zelandoperla* sp.) and fragments of *Cratoneuropsis relaxa* in the gut of a *Limonia hudsoni* larva (x50).

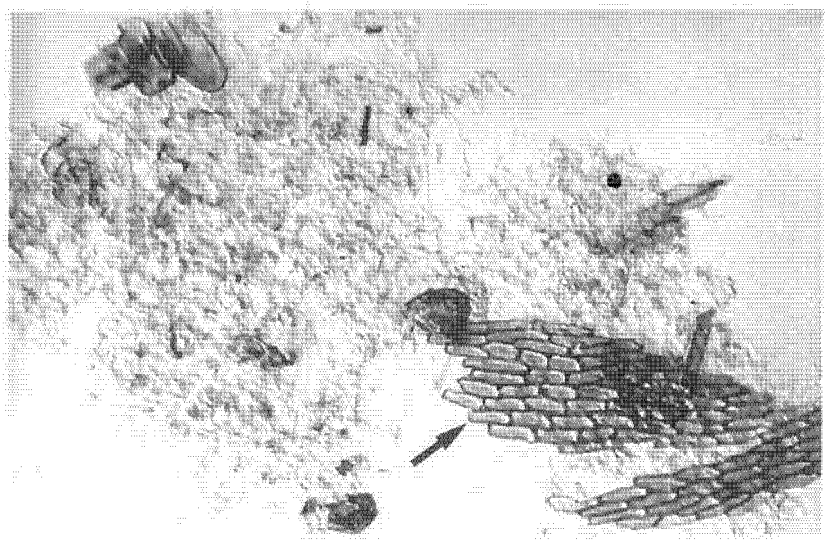


Fig.5: Gut contents of a *Zelandoperla* larva showing amorphous detritus with no cellular detail apparent, and a fragment of *C. relaxa* leaf (arrowed), (x200).

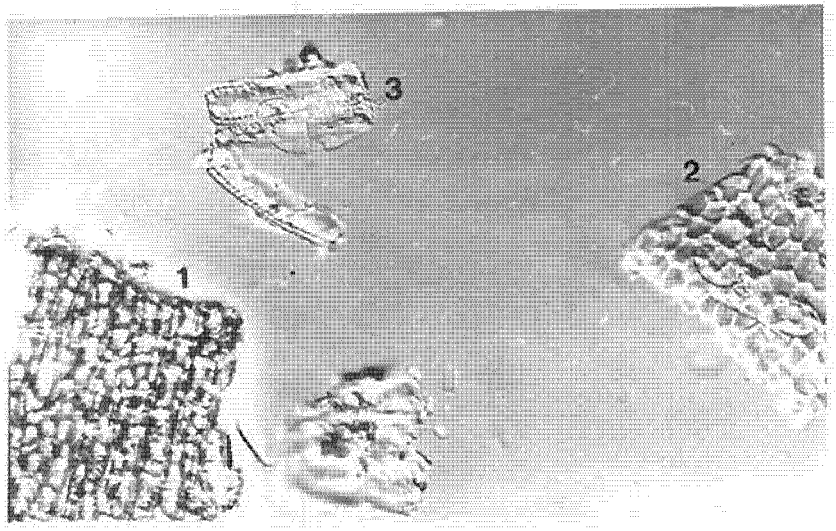


Fig.6: Gut contents of *Austroperla cyrene* larvae showing unconditioned riparion vegetation (possibly a beech leaf (1)), fragments of an unidentified liverwort (2) and the diatom *Epithemia* (3), (x200).

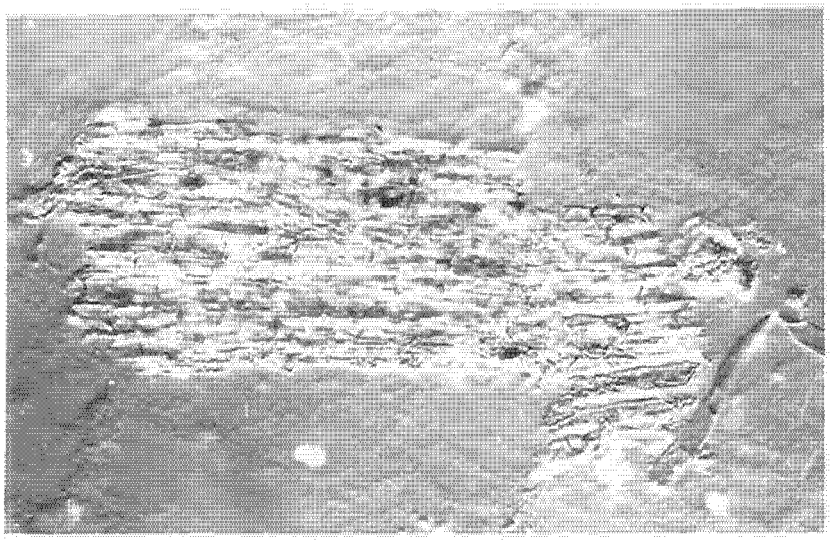


Fig.7: Gut contents of *Limonia hudsoni* showing conditioned riparian plant material. Note the less distinct shape of the cells indicating that it may have been in the stream some time (x200).

Table 1: The 6 food categories recognised in gut contents. Where possible food items were identified to subcategories, either on a taxonomic or particle size basis.

CATEGORIES		SUB-CATEGORIES	
1	**Bryophytes**	*Cratoneuropsis relaxa*) *Fissidens rigidulus*) (Mouse Stream) *Bryum blandum*)	
		Plagiochila retrospectans) (Tim's Creek) *Hepatostolonophora paucistipula*)	
		Bryophyte rhizoids	
2	**Algae**	Filamentous septate (branched) Filamentous septate (unbranched) Filamentous non-septate (branched) Filamentous non-septate (unbranched)	
		Cyanobacteria - *Chamaesiphon* sp.	
		Bacillariophyta *Diatoma hiemale* var. *mesodon* *Surirella* sp. *Tabellaria* sp. *Fragilaria* sp. *Gomphonema olivaceum* *Navicula* sp. *Melosira* sp. *Epithemia sorex* *Cymbella* sp. *Cocconeis* sp. *Synedra* sp. 5 unidentified genera (rarely found)	
3	**Fungi**	Hyphae and spores	
4	**Vascular Plants**	- decomposed - fresh	
5	**Detritus**	- FPOM (Fine Particulate Organic Matter) <75 μm - SPOM (Small Particulate Organic Matter) 75-250 μm - MPOM (Medium Particulate Organic Matter) 250-1000 μm	
6	**Animals**	- invertebrate remains	

plants and as decaying material in stream channels. Algae were scraped from artificial substrata (grass carpet covered tiles) placed 2 months previously in Mouse Stream. Bryophytes were visually free of periphyton, and this was checked in the laboratory where plants were examined microscopically (x20 magnification); bryophytes supporting obvious periphyton were rejected.

Invertebrates for stable carbon analysis were some of those animals used for gut content analysis. Only heads, legs and empty abdomens were analysed to avoid possible contamination by gut contents. Animal material was washed twice in distilled water to remove any adhering fine particulate matter. All material was air dried (60°C, 24 h) and sent to D.S.I.R. Institute of Nuclear Sciences for analysis by mass spectrometry (see Rounick *et al.* 1982).

Biochemical analysis of plants

An indication of the food value of bryophytes was obtained by comparing their proximate composition with samples of living and decomposing riparian plants. Bryophytes analysed from Mouse Stream were the mosses, *Fissidens rigidulus*, *Cratoneuropsis relaxa* and *Bryum blandum*, whereas the liverworts *Plagiochila retrospectans* and *Hepatostolonophora paucistipula* were analysed from Tim's Creek. Riparian plant materials taken for comparison were lamellae of the tussock grasses *Chionochloa pallens* and *C. flavescens*, leaves of the hebes, *Hebe subalpina* and *H. odora*, and beech leaves, *Nothofagus solandri* var *cliffortioides*, fronds of *Blechnum capense* and lamellae of the reed *Marsippospermum gracile*. The first four plants listed were from the Mouse Stream catchment and the others from alongside Tim's Creek.

In July 1989, samples of riparian vegetation were collected from 5 to 10 individual plants at each site and subsequently decomposed. Grass lamellae and fern fronds were cut into small (5 cm long) segments and placed into separate open ended PVC tubes (10 cm long, 4 cm diameter) which were sealed with netting (0.5 mm mesh). Hebe and beech leaves were removed from their stems and placed into separate tubes. All containers were anchored with weights and left in their respective streams for a 2-month conditioning period. Materials not used in decomposition studies were frozen (-20°C) in plastic bags in the dark to prevent sample degradation (Allen *et al.* 1974).

Following collection of conditioned material, all samples were freeze-dried. Decomposed material selected for analysis was free of detritus, but would have been colonized by microflora active in the decomposition process. Material was then homogenised in a Cyclotec 1093 sample mill (0.4 mm mesh) and stored in capped plastic cups.

The food value of all material collected was assessed by proximate analysis. Quantities of eight compounds were analysed, of which five (lipid, soluble carbohydrate, starch, nitrogen and energy content) can be regarded as indicating food quality. Of the other three, holocellulose and fibre are structural elements of

plants that usually have low food value, and ash is a reflection of the amount of inorganic (and therefore largely indigestible) material in the plant.

Concentrations of crude fat, soluble carbohydrate, cellulose (as holocellulose) crude fibre and starch were determined as described by Allen *et al.* (1974). Ash content was measured following ashing of pre-weighed, dry material in a muffle furnace (550°C, 12 h). Energy content (as kilojoules) was assessed by bomb calorimetry (Gallenkamp) and total nitrogen determinations were made by nuclear magnetic resonance (NMR) spectrometry in the Soil Science Department, Lincoln University. Crude protein concentration was estimated by multiplying total nitrogen values by 6.25 (Allen *et al.* 1974). Analyses were conducted in triplicate on all materials except for NMR nitrogen analyses. The latter were carried out in duplicate on five plant samples.

RESULTS

Gut Analysis

General survey

Twenty three taxa were examined, five of which were characteristic of bryophyte habitats and three of riffles (Chapter 2). The other 15 taxa, although not characteristic of the bryophyte fauna were often associated with these plants. Although bryophyte fragments were found in guts of 14 species, the frequency of occurrence of this material was minimal in most animals (Table 2). The principle exceptions to this were the tipulid *Limonia hudsoni* and the oeconesid caddisflies *Zelandopsyche ingens* and *Oeconesus similis* (Table 2). Detritus was the dominant food material consumed by all species examined at each site, although the frequency of occurrence of algae, fungi and riparian vegetation was also relatively high.

The frequency of occurrence of each food material present in the guts of all invertebrates differed between sites: the frequency of algae compared to other material in guts of animals (all species pooled) at Mouse Stream was higher than that at Tim's Creek (frequency of algal occurrence = 15% at Mouse Stream, 3% at Tim's Creek; $F = 46.17$, $p<0.001$). The dominant algal taxa ingested also differed at each site: thus, *Diatoma* (39%), *Tabellaria* (24%) and *?Melosira* (16%) dominated at Mouse Stream whereas *Epithemia* was the most abundant taxon in gut contents at Tim's Creek (31%). The diatoms *Cocconeis*, *Chamaesiphon*, *Navicula* and *Gomphonema* were also common constituents of gut contents at Mouse Stream, and *Cocconeis*, *Chamaesiphon* and *Diatoma* were also eaten at Tim's Creek.

The percentage of bryophyte material ingested by all invertebrates did not differ between sites ($F= 2.21$, $p>0.05$), but the material consumed reflected the relative commonness of bryophyte species at each site. At Mouse Stream, *C. relaxa* was the most commonly consumed moss and occurred in 60% of guts, whereas liverworts were present in 35% of guts of animals from Tim's Creek. Another moss, *F. rigidulus*, was

Table 2: Percentage of occurrence of bryophyte fragments compared to other food types found in the guts of 23 invertebrate taxa with. - = not examined. * = identification of smaller instars based on the occurrence of larger instars in the same habitat.

Taxa	Unshaded site		Shaded site	
	n	%	n	%
Diptera				
Muscidae sp. A	11	0	-	-
Empididae sp. A	12	0	-	-
Empididae sp. B	-	-	37	0.5
Limonia hudsoni (Edwards)	38	26.4	19	20.6
Paralimnophila skusei Hutton	-	-	6	0
Austrosimulium ungulatum Tonnoir	-	-	15	2.0
Chironomidae	27	0	34	0
Ephemeroptera				
Nesameletus sp.	9	0	-	-
Deleatidium sp.	81	0.4	7	0
Trichoptera				
Oeconesus similis Mosley	7	7.5	5	3.7
Zelandopsyche ingens Tillyard	-	-	6	8.4
Zelolessica cheira McFarlane	-	-	17	2.7
Hydrobiosis silvicola McFarlane	9	0	-	-
Plecoptera				
Acroperla spiniger (Tillyard)	47	1.7	-	-
A. trivacuata (Tillyard)	-	-	20	3.2
Cristaperla fimbria (Winterbourn)	12	0	18	0
*Zelandoperla fenestrata** Tillyard	99	1.8	54	0.8
*Zelandobius unicolor** Tillyard	128	2.7	-	-
Austroperla cyrene (Newman)	-	-	58	1.7
Halticoperla viridans (McLennan & Winterbourn)	-	-	4	0
Coleoptera				
Orchymontia calcarata ordish	-	-	60	0.3
Helodidae	-	-	5	0.8
Isopoda				
Stylotiscus otakensis (Chilton)	-	-	6	0

present in a similar number of guts at both sites (29% at Mouse Stream, 27% at Tim's Creek).

Fungi and detritus in guts of all species combined differed between sites (F= 15.2, fungi; F= 7.17, detritus, $p<0.01$), and these items occurred at a greater frequency in animals from Tim's Creek than Mouse Stream (x= 3.7% fungi, x= 83% detritus at Tim's Creek ; x= 0.4% fungi, x= 75% detritus at Mouse Stream).

Diets of specific animals: habitat and site differences

To determine whether animals ingested different materials in different habitats, the gut contents of selected taxa that were present in high numbers in riffles and amongst bryophytes at either site and which were known to consume bryophytes were examined. Only four of the 22 taxa met these requirements. Of these, guts of the larvae of *Deleatidium* sp., *Zelandobius* sp. and *A. spinlger* from bryophyte samples at Mouse Stream contained significantly more algae than those from riffles (t= 13.7, 2.57, 2.68, respectively, $p<0.05$) and significantly less detritus (t= 26.15, 2.97, 2.78; $p<0.05$, Figs 8a-c). Larvae of the fourth species, *Austroperla cyrene* taken from bryophyte samples at Tim's Creek had eaten more riparian plant material and less detritus than larvae collected in riffles (t= 2.59, riparian vegetation; t= 2.27, detritus, $p<0.05$; Fig. 8d).

Only 2 taxa, *Limonia hudsoni* and *Zelandoperla* sp. ingested bryophytes and were common in both streams. Bryophyte material was more abundant in guts of *Limonia* larvae at Mouse Stream, and terrestrial plant fragments were more abundant in those from Tim's Creek (t= 2.35, bryophytes; t= 3.55, riparian vegetation, $p<0.05$; Fig. 9a). Larval *Zelandoperla* guts contained more algae at Mouse Stream (t= 4.28, $p<0.01$), but riparian plant material, fungi and detritus made up a greater proportion of gut contents at Tim's Creek (t= 2.76, 2.68, 2.29, respectively; $p<0.05$; Fig. 9b).

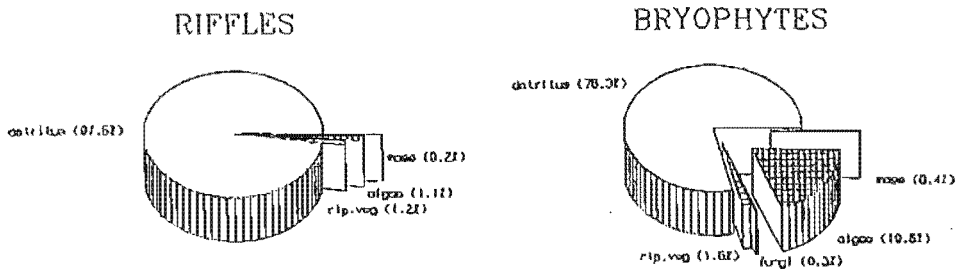
Stable Carbon Analysis

Plant material

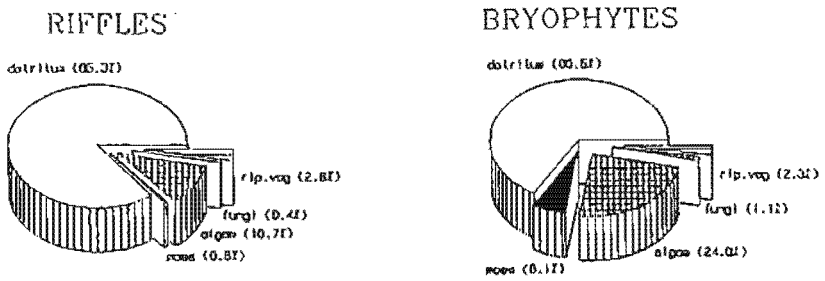
Stable carbon ratios of aquatic bryophytes and algae from Mouse Stream were more depleted in ^{13}C than the two terrestrial plants, tussock and hebe (Fig. 10a). Of the mosses, *C. relaxa* was the most depleted in ^{13}C (-35.5°/oo) and *F. rigidulus* the least (-30.3°/oo); the alga *Diatoma* had an intermediate $^{13}C/^{12}C$ ratio (-31.1°/oo).

Differences in $^{13}C/^{12}C$ ratios between aquatic and terrestrial plants from Tim's Creek were smaller than at Mouse Stream (Fig. 10b), and although ratios for the mosses *Pterygophyllum* and *Fissidens* were most lowest, they were only 2-3°/oo more depleted in ^{13}C than those of beech leaves (-29.3°/oo) and the liverwort *P. retrospectans* (-29°/oo). Detritus from this site was most enriched (-28.1°/oo), suggesting predominantly allochthonous origins.

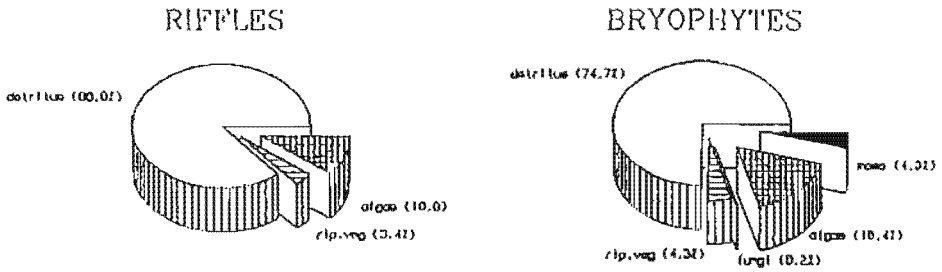
a Deleatidium



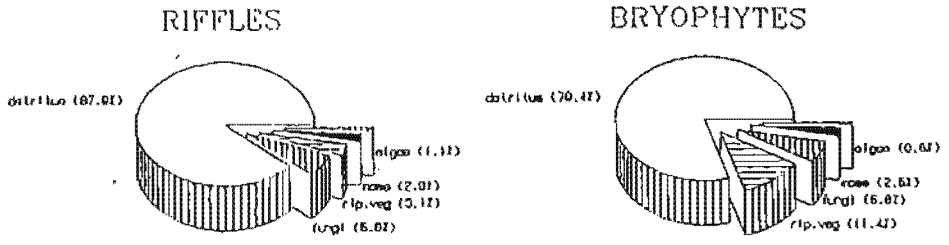
b Zelandobius



c Acroperla spiniger



d Austroperla cyrene



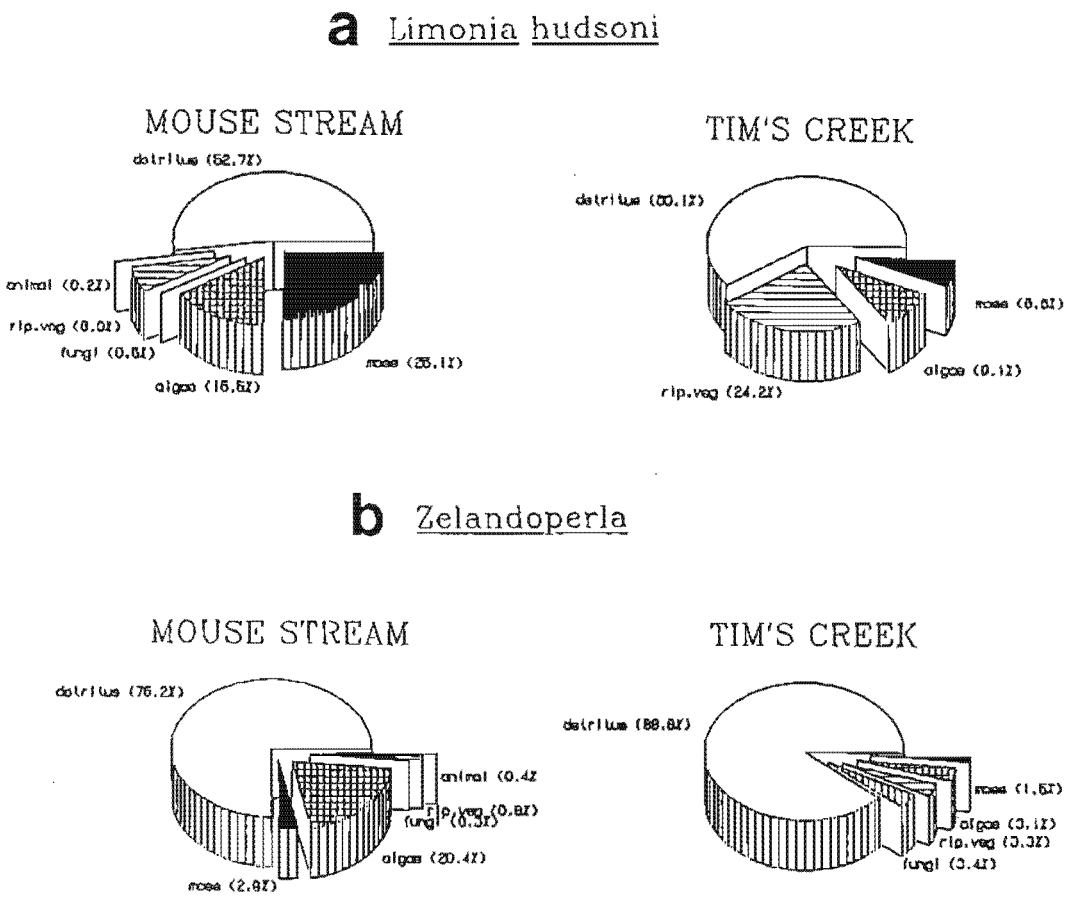
Figs 8: Percentages of 6 food types in guts of selected taxa collected from riffle and bryophyte habitats in the two study streams.

a, *Deleatidium* larva from Mouse Stream

b, *Zelandobius* larva from Mouse Stream

c. *Acroperla spinlger* larva from Mouse Stream

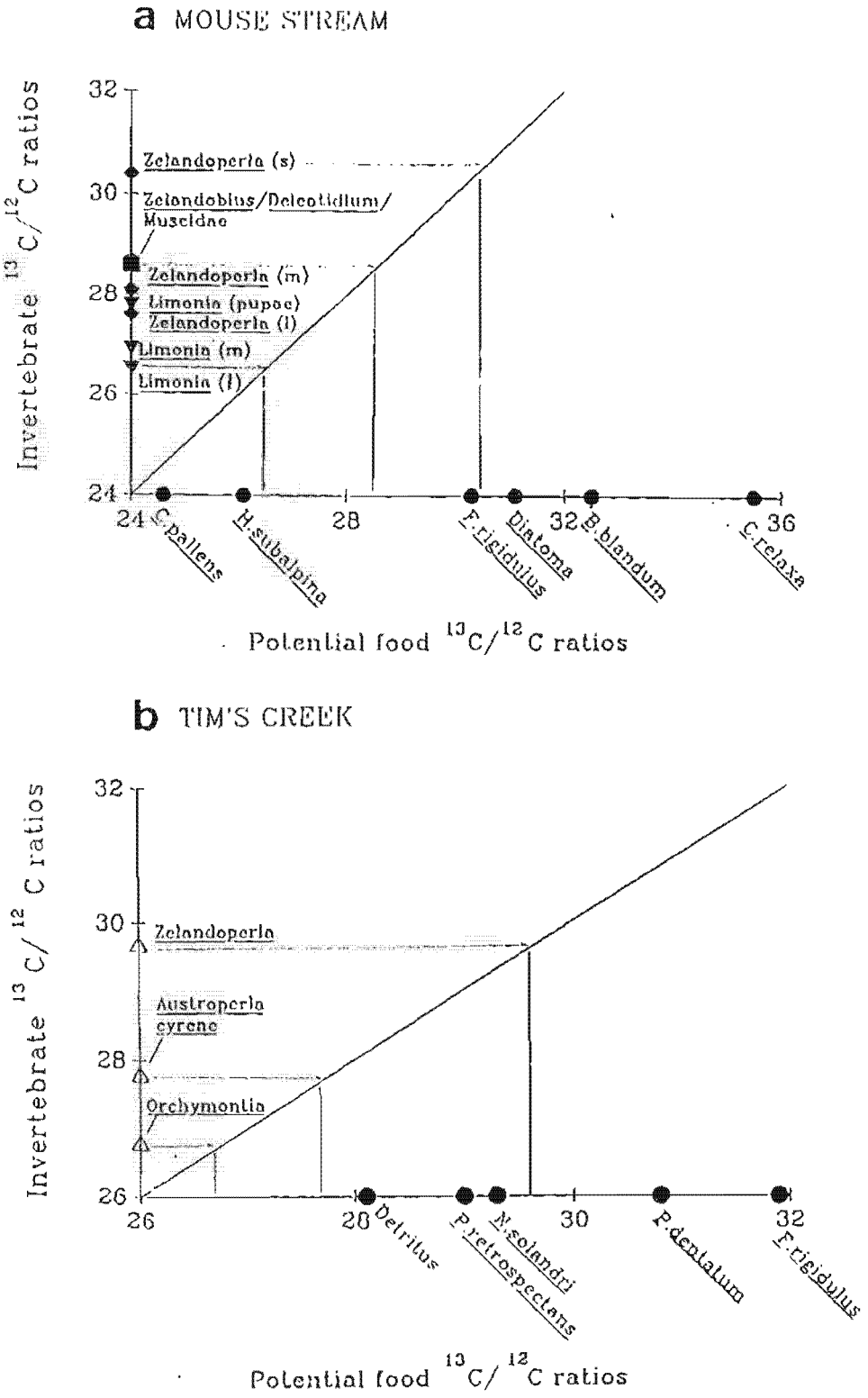
d. *Austroperla cyrene* larva from Tim's Creek



Figs 9: Percentages of 6 food types found in guts of selected taxa collected from bryophytes in the two study streams.

a, *Limonia hudsoni* larva from Mouse Stream and Tim's Creek.

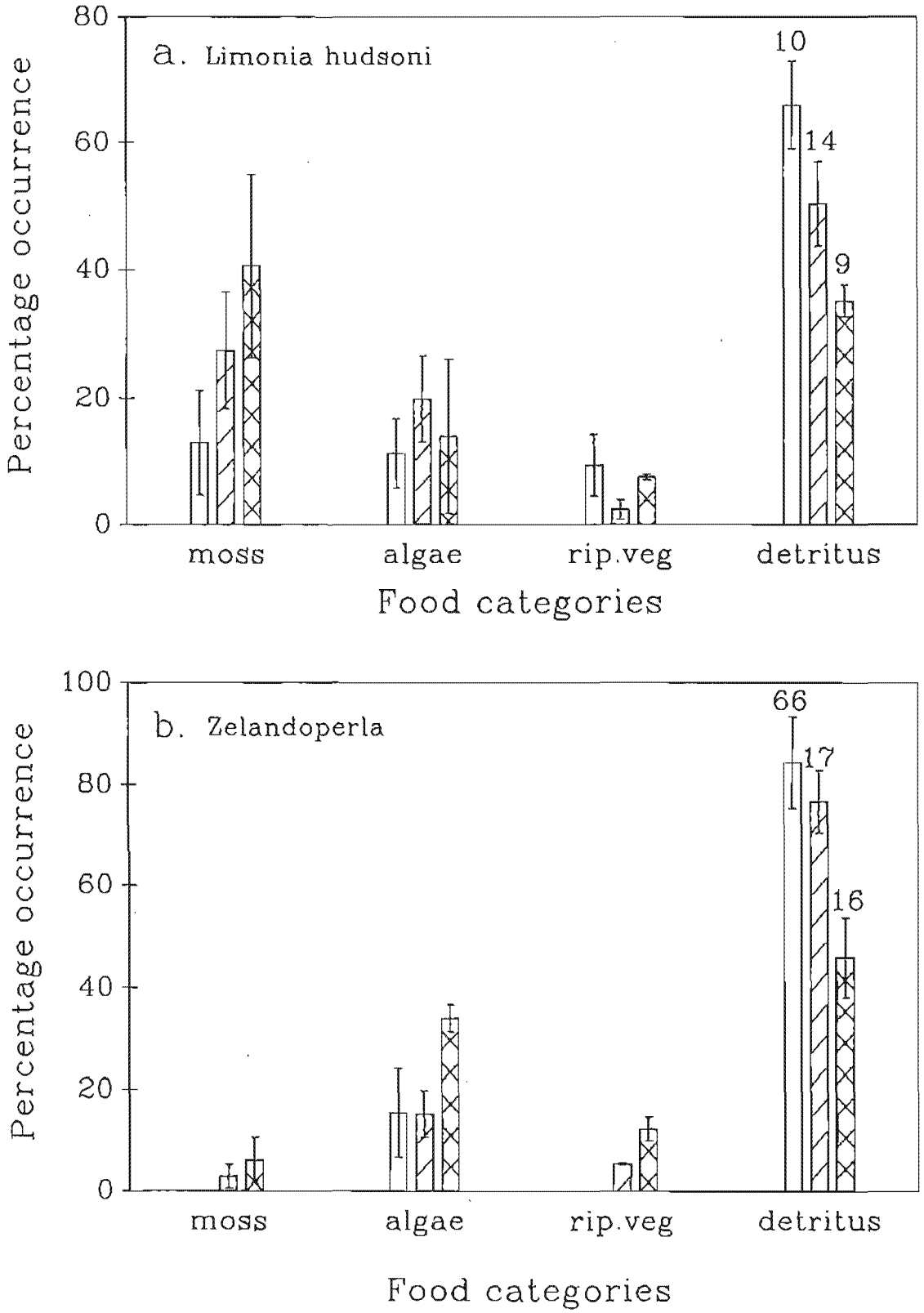
b, *Zelandoperla* larva from Mouse Stream and Tim's Creek.



Figs 10: $^{13}C/^{12}C$ ratios of some potential food items (x - axis) and invertebrate taxa (y-axis) from each stream. Relationships between $^{13}C/^{12}C$ ratios of animal tissues to ratios of plant material are indicated by the horizontal and vertical lines, illustrating the potential foods eaten by an animal to obtain a particular $^{13}C/^{12}C$ ratio. Sizes of a *Zelandoperla* and *Limonia hudsoni* varied and were qualitatively assigned to small (s); medium (m), and large (l) sizes based on head-width measurements.

a. Mouse Stream

b. Tim's Creek



Figs 11: Percentage occurrence of 4 food categories in small, medium, and large larvae of a) *Limonia hudsoni*; and b) *Zelandoperla*. Open bars = small larvae; crossed bars = medium larvae; hatched bars = large larvae ($\bar{x} \pm 1$ SE; number of individuals of each size is given above the values for detritus).

Animal material

Of the invertebrates taken from Mouse Stream, $^{13}C/^{12}C$ ratios of large *Limonia* larvae were most enriched (-26.5°/oo), and those of small *Zelandoperla* larvae were most depleted in ^{13}C (-30.4°/oo). These $^{13}C/^{12}C$ ratios were, however, all more depleted than those of riparian vegetation (Fig. 10a). Because detritus was the dominant item consumed by these animals at Mouse Stream according to gut analysis, it seems likely that this was primarily of autochthonous origin.

Stable carbon isotope ratios of both *Zelandoperla* and *Limonia* larvae were higher (less depleted in ^{13}C) in larger animals (Fig. 10a), suggesting greater consumption, and/or enhanced assimilation of riparian vegetation with age. Gut analysis of larvae, however, indicated that less detritus, but more algae (*Zelandoperla*) and bryophyte material (*Limonia*) was ingested by larger larvae (Figs 11a,b). Thus the two methods were not entirely consistent with each other and suggests there were differences between what was consumed, and what was actually assimilated, by animals.

Of the three taxa taken from Tim's Creek, *Zelandoperla* larvae were most depleted in ^{13}C. Ratios of both *Austroperla cyrene* and *Orchymontia dispersa* were more enriched than beech leaves and detritus from this site (Fig. 10b), and suggest that the detritus that comprised a major portion of their diets was largely of terrestrial origin. *Zelandoperla* larvae, in contrast, consumed significant amounts of algae (Fig. 9), which has a lower $^{13}C/^{12}C$ ratio than beech. Gut analysis indicated that these stonefly larvae had a mixed algal-detrital diet, and this is consistent with the stable carbon data.

Plant Analysis

1. Fresh riparian plant material

Hebes from Mouse Stream had higher percentages of lipid, soluble carbohydrate, starch and nitrogen, and a higher energy content than either of the tussocks, but less fibre and holocellulose (Table 3). Ash content of all these plants was between 3.2% and 5.2% dry weight.

Beech from Tim's Creek contained more lipid and starch, and had a higher energy content than either the fern (*Blechnum*) or the rush (*Marsippospermum*). Beech leaves, however, had less holocellulose, fibre and ash than these plants (Table 3). *Marsippospermum* contained most holocellulose and fibre, and *Blechnum* had the highest ash content (Table 3).

High amounts of lipid, soluble carbohydrate, starch, nitrogen and energy content indicate a plant is likely to be a "good" food source for herbivores, whereas high concentrations of the more refractory compounds holocellulose and fibre, and inorganic ash, are indicative of "poorer" food. At Mouse Stream, the two species of hebe thus represent "better" foods than the tussock grasses, but the relative food value of plants from Tim's Creek was is not as well defined. Although beech leaves contain

Table 3: Results of proximate analyses of selected plants potentially available as food to invertebrate consumers in Mouse Stream and Tim's Creek. Riparian plants were analysed in the following state; freshly picked (F) or following a two month conditioning period (D) in each stream. All bryophytes were free of detritus and periphyton. Results are means of triplicate samples analysed for each food; some plants were not analysed for certain constitutents (NA).

Plant		Lipid (%)	Carbohydrate (%)	Energy (J/g)	Starch (%)	Nitrogen (%)	Protein (%)	Holocellulose (%)	Fibre (%)	Ash (%)	Totals* (%)
TRACHAEOPHYTA											
Chionochloa flavescens	F	3.9	4.6	23.8	0.4	0.9	6.1	38.9	26.6	4.1	85.5
	D	2.5	2.2	23.9	0.3	1.1	6.9	46.6	24.5	4.5	88.7
Chionochloa pallens	F	2.6	2.9	19.1	0.3	0.9	5.9	40.7	24.5	3.8	81.6
	D	2.7	1.6	N/A	0.4	1.1	6.8	44.3	25.3	3.8	86.0
Hebe subalpina	F	5.3	11.6	25.7	2.1	1.1	7.0	20.1	11.5	5.2	63.9
	D	5.1	8.4	26.7	1.6	1.4	8.7	37.6	10.2	4.6	77.6
Hebe odora	F	10.2	10.3	26.7	2.2	1.1	6.8	23.2	13.2	3.2	70.2
	D	12.7	8.9	29.6	1.6	1.3	8.0	39.8	19.9	4.9	97.1
Nothofagus solandri var *cliffortioides*	F	7.5	4.7	25.3	1.6	0.9	5.9	31.2	21.8	3.3	76.9
	D	5.9	3.4	22.6	1.3	1.0	6.0	40.0	25.3	4.2	87.1
Marsipospermum gracile	F	3.4	5.1	21.0	0.7	1.4	8.4	38.5	23.9	9.5	90.9
	D	2.7	3.6	NA	0.9	1.5	8.9	44.6	20.3	7.7	90.2
Blechnum capence	F	2.3	5.3	20.6	1.5	1.1	7.0	34.5	23.6	7.2	82.5
	D	1.9	4.6	NA	NA	1.1	6.6	NA	21.8	8.3	
BRYOPHYTA											
Fissidens rigidulus		1.6	3.1	19.5	1.3	2.3	14.1	39.1	26.5	6.0	94.0
Cratoneuropsis relaxa		2.0	1.4	20.4	1.4	1.5	9.2	38.4	32.7	7.7	94.3
Bryum blandum		1.9	5.9	20.8	1.4	2.1	12.7	50.1	22.0	11.8	107.9
Plagiochila retrospectans		2.7	2.6	21.4	0.9	1.1	6.9	50.1	23.8	7.4	95.5
Hepatostolonophora paucistipula		3.8	3.9	23.7	1.1	1.1	6.9	34.7	27.7	7.4	86.6

*Totals exclude energy values and were often less than 90%, reflecting contribution of unanalysed compounds (e.g., α - cellulose, hemicellulose, reducing sugars) to dry weight.

higher quantities of lipids and starch and have a greater energy content, they contain less soluble carbohydrate and nitrogen than either the fern or the rush. Because they contain more refractory materials, however, they may be of lower overall food value.

2. Effects of decomposition

Major differences existed in fates of the different food compounds when fresh plant material was allowed to undergo a two month "conditioning" period in each stream. Reductions in lipid, soluble carbohydrate and starch content were generally observed in conditioned plants, whereas increases in nitrogen and energy content were observed in most instances (Table 3). Structural components (holocellulose and fibre) and the inorganic ash fraction of plants showed no consistent change in mass after 2 months of decomposition.

3. Bryophytes

Quantities of lipid, soluble carbohydrate and starch were usually lower in bryophytes than in the riparian plants analysed, although mosses at Mouse Stream contained higher proportions of soluble carbohydrate and starch than the tussock *C. pallens*. Concentrations of nitrogen in all mosses from Mouse Stream were higher than in any riparian plants from that site (Table 3), but were lower in the liverworts than either the fern or the rush from Tim's Creek. Energy content of mosses from Mouse Stream was lower than that in all riparian plants (except *C. pallens*) collected here and lower than in liverwort, fern and rush collected from Tim's Creek.

Of the structural components, mosses contained more holocellulose and fibre than both species of hebe, and more ash than all riparian plants. These structural components were also a major component of the liverworts at Tim's Creek, although both the rush and the fern contained higher amounts of holocellulose and ash, respectively.

Bryophytes usually contained less easily digestible, and more refractory compounds than most of the riparian plants (tussock was the exception) suggesting that they represented a potentially less "nutritious" food source for invertebrates than the other plants.

No clear differences in proximate food value between mosses and liverworts were evident, although lipid and energy contents of liverworts were higher, and their starch and nitrogen contents were lower. Structural components of both subclasses were similar, although *Bryum* contained more holocellulose and less fibre than the other bryophytes, and *Cratoneuropsis* had the highest fibre content.

DISCUSSION

Many New Zealand alpine streams are constantly exposed to generally unpredictable, heavy rainfall. Consequently, stream discharges exhibit great temporal variability and streambed instability is often high. Allochthonous inputs in the form of windblown leaves and other riparian vegetation are low, and retention of this material is poor, as in sub-alpine streams in Westland (Winterbourn 1986, Graesser 1988 Winterbourn *et al.* 1988). Enhanced environmental stability provided by bryophytes in these streams is postulated to explain high invertebrate densities in this habitat (Chapter 2), and indeed some taxa are found only within bryophytes. A potential consequence of a close association between bryophytes and invertebrates is increased grazing pressure on the plants, yet this does not appear to be so.

Consumption of bryophytes by New Zealand stream invertebrates appears to be very low, especially considering the diversity and abundance of animals that colonise these plants. The 22 taxa examined came from five insect and one crustacean order, and represented 17 families. Of these, only three taxa, *Limonia hudsoni*, *Zelandopsyche ingens* and *Oeconesus similis* , appeared to consume bryophytes with a high degree of frequency. Furthermore, only the larvae of *L. hudsoni* contained large amounts of bryophyte material in their guts, this being up to 60% of total gut contents on occasions (unpublished data).

It has been postulated that macrophytes act as substrata for periphyton, which is in turn grazed by invertebrates (e.g., Hutchinson 1975, Rogers & Breen 1983, Thomas 1987). Growth of periphyton can be enhanced by the release of dissolved organic matter (DOM) and plant nutrients from cells of the plants (Wetzel 1969, 1983, Allen 1971). Aquatic bryophytes in contrast to angiosperms have no conducting or transporting tissues, no root systems, and leaves that are only one cell thick and covered with a thin waxy cuticle. Although small quantities of DOM may leak from individual bryophyte cells, this would be much less than expected from macrophytes (e.g., Pomogyl *et al.* 1984, Best & Dassen 1987), which have a large-scale transport of material around their tissues and have holes in their leaves (i.e., stomata), effectively exposing the thin-walled mesophyll and pallisade cells to the surrounding water. Thus it seems unlikely that DOM produced by bryophytes could play as important a role in affecting periphyton growth as that produced by some macrophytes (Best *et al* 1990). Nevertheless, periphyton is often abundant on bryophyte stems and leaves, and may reduce potential grazing pressure on the plant tissues themselves.

Algal standing crops were lower at Tim's Creek than Mouse Stream, and if the above hypothesis were correct, one might have expected that bryophytes at Tim's Creek would face greater grazing pressures than those at Mouse Stream. However, examination of gut contents from selected taxa at both streams indicated this was unlikely to be the case and indeed liverworts at Tim's Creek were consumed less frequently than mosses at Mouse Stream. The abundant fine detritus trapped by

bryophytes provides a further alternate food source for invertebrates, and its utilization may also reduce grazing pressure on the plants.

Despite the fact that alternative food sources are often associated with bryophytes, they are consumed by some taxa. Larvae of *Limonia* appear to have only a limited capacity to move amongst stones and gravel, and bryophytes provide them with a stable microhabitat sheltered from the current and into which they can burrow. If morphological constraints confine *Limonia* larvae to this habitat, then it may be advantageous for them to be able to consume as many of the alternative food sources found there as possible, including the bryophytes themselves.

Plants are known to contain a wide variety of chemicals that can deter invertebrate consumption. These were categorized as "digestibility reducers" or toxins and were regarded as being characteristic of "apparent" and "unapparent" plants, respectively (Feeny 1976, Rhoades & Cates 1976, Rosenthal & Janzen 1979). I regard bryophytes in alpine streams as highly "apparent" to the invertebrates dwelling amongst them and as such the production of digestibility reducing compounds such as tannins, lignins and other polyphenols should be favoured. However, although species of *Andreae* (Family Andreaeidae) contain tannins in their cell walls (Schofield 1985), and materials closely related to lignin have been isolated from some moss genera (e.g., *Sphagnum, Dawsonia*; Markham & Porter 1978), most bryophytes do not possess the digestibility reducers.

On the other hand, many biologically active chemicals including some intensely pungent or bitter compounds, have been isolated from a variety of liverworts (e.g., Suire *et al.* 1975, Markham & Porter 1978, Asakawa & Heidelberger 1982). Two of these compounds, Plagiochiline A and Plagiochiline I, isolated from a variety of *Plagiochila* species, were found to be extremely potent antifeedants when tested against the African army worm (Asakawa and Heidelberger 1982). In this context, it is therefore interesting to note that the common liverworts *Plagiochila retrospectans* and *Hepatostolonophora paucistipula* that dominate the bryoflora at Tim's Creek made up only 2% of the diet of *Limonia* at this site, whereas the mosses that predominated at Mouse Stream made up a significant (57%) proportion of their gut contents.

As well as being poor food sources due to the presence of potential antifeedant compounds, bryophytes appear to be generally inferior foods in nutritional terms compared with a number of common riparian alpine plants. The results of my proximate analyses indicated comparatively high levels of structural compounds in bryophytes, and relatively low quantities of more easily digested compounds such as starch, soluble carbohydrate and lipid. Thus, consumers of bryophytes are likely to need particularly effective digestive mechanisms if they are to successfully cope with food dominated largely by refractory structural polymers.

Some larval tipulids have a very high midgut pH (Sinsabaugh *et al.* 1985, Barlocher & Porter 1986) which helps enhance digestibility of celluloses and hemicelluloses (Terra 1990). They may also contain large populations of endosymbiotic

bacteria in their hindguts that can digest these structural materials (Sinsabaugh *et al.* 1985, Griffiths & Cheshire 1987, Terra 1990). Thus, despite their relatively low nutritional value, bryophytes may still represent a valuable food source to *Limonia* larvae. The larvae of *Limonia nigrescens* (Hutton) are known to possess cellulase activity (Winterbourn 1982a), but nothing is known about the digestive capabilities of *L. hudsoni*. Thus although bryophyte fragments were common in guts of these animals, they may not necessarily be digested by these animals. Although bryophyte consumption by stoneflies has been reported (e.g., *Ptenoarcella badia*, Fuller & Stewart (1977), *Zapada columbiana*, Mutch & Pritchard (1984b)), *Zelandoperla* larvae which are characteristic inhabitants of bryophyte mats, do not appear to rely on them greatly for food.

Bryophagy is also known in limnephilid caddisflies, (Williams & Williams 1982, Mutch and Pritchard 1984a) and I found that the primarily detritivorous larvae of *Zelandopsyche ingens* (Winterbourn & Davis 1976, Winterbourn 1982a), also ingested bryophytes. Although not quantitatively assessed because only a few larvae occurred in my collections, the moss *Fissidens rigidulus* was sometimes prominent in guts. This concurs with observations by Winterbourn & Davis (1976), who found that *Z. ingens* ate *F. rigidulus* in laboratory trials. Of particular interest was their finding that larvae did not ingest case material (an alternative food) when offered moss in contrast to other foods of low attractiveness (i.e., yellow leaves, and clean twigs of *Nothofagus solandri* var *cliffortioides*).

CONCLUSIONS

Bryophytes are persistent features of many New Zealand alpine streams and represent stable habitats for invertebrates. Consequently, discrete invertebrate assemblages are found within bryophytes, often at high densities. In contrast to highly unstable riffles, the accumulation of detritus and periphyton is greatly enhanced by the presence of bryophytes.

Invertebrates dwelling amongst these plants can consume three principal categories of foods: algae, detritus and the bryophytes themselves. Of the 23 invertebrate taxa for which gut contents were analysed, most had mainly consumed algae and detritus, and bryophagy was restricted to three taxa, *Limonia hudsoni*, *Zelandopsyche ingens* and *Oeconesus similis*. Avoidance of bryophyte tissues is postulated to be a consequence of their low nutritional value, the presence of alternative foods, and the likely existence of antifeedant compounds. In this respect it was notable that *Limonia hudsoni* consumed liverworts less often than mosses, a finding that may reflect the presence of strong antifeedant compounds in liverwort tissues.

CHAPTER SEVEN:

BRYOPHYTE ENHANCEMENT OF AUTOTROPHIC PRODUCTION

IN ALPINE HEADWATER STREAMS

INTRODUCTION

Forested headwater streams are often considered to be predominantly heterotrophic, with their primary biological energy source being derived from the surrounding catchment (e.g., Fisher & Likens 1973, Cummins 1974). Autotrophic production by periphyton is usually small in heavily shaded streams (Fisher and Likens 1973, Cowie 1980, Bott *et al.* 1985, Mayer & Likens 1987, Feminella *et al.* 1989) primarily because incident light levels are low (Lyford & Gregory 1975). Not surprisingly, the removal of surrounding vegetation by clearcut logging has often been found to increase periphytic productivity in streams where nutrients are not limiting, and in turn increases in invertebrate productivity and diversity have resulted (Murphy & Hall 1981, Feminella *et al.* 1989).

The importance of leaf processing by invertebrates in headwater streams is well known (e.g., Cummins 1973, 1974, Hynes 1975, Bird & Kaushik 1981, Cummins *et al.* 1989), and interactions between invertebrates and allochthonous inputs can show seasonal patterns. These can reflect the predictable nature of autumnal leaf fall in the Northern Hemisphere (e.g., Boling *et al.* 1975), or seasonal rainfall and stream discharge patterns that may greatly affect stream retention characteristics (Anderson *et al.* 1976, Dance 1981).

Many New Zealand headwater streams occur on steep terrain and are subject to heavy and frequent precipitation. Although litter fall from the surrounding forest may well be seasonal (Winterbourn 1976), retention of this material is often low (Graesser 1988). Algal productivity in such forested streams is also low (Cowie 1980), and indeed even in open headwater streams above the tree-line, algal standing crops and productivity may be adversely affected by substrate instability and streambed scouring particularly during periods of heavy flooding (Scrimgeour *et al.* 1988, Scrimgeour & Winterbourn 1989, Biggs & Close 1989, Graesser 1988). Poor retention of coarse particulate organic matter coupled with the variable availability of periphytic algae seem to explain why many New Zealand stream invertebrates seem to feed principally on thin but persistent stone-surface biofilms and fine particulate organic matter trapped

amongst bed sediments (Cowie 1980, Rounick 1982, Rounick & Winterbourn 1983, Winterbourn 1986).

Although autotrophic algal production in forested headwater streams is often very low, aquatic bryophytes are frequently common (Glime 1968a, Slack & Glime 1985, Sheath *et al.* 1986) on stable substrates and in turbulent water (McAuliffe 1983). Because they often form extensive mats in these habitats, they can be expected to play a major role in stream metabolism, as suggested by Johnson (1978) and Naiman (1983).

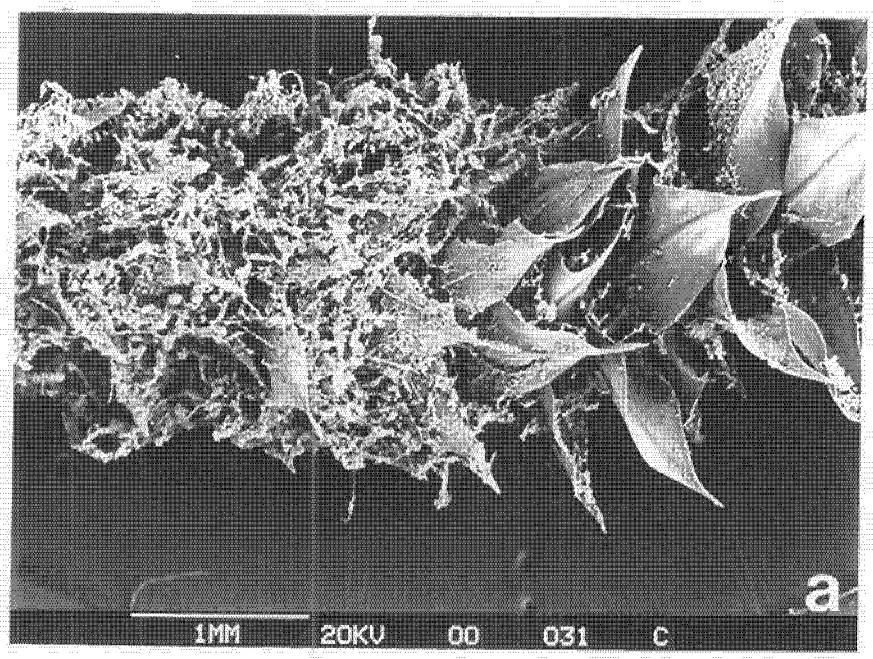
In the present study, biomass fluxes of algae, detritus and bryophytes were examined in two contrasting alpine streams, one above the tree-line and one within beech forest. Because it was known that periphyton can colonise bryophytes extensively (Chapters 4 & 5; Figs 1 a-d), I also investigated whether the presence of bryophytes enhanced periphyton biomass.

MATERIALS AND METHODS

1 Algal productivity

Artificial substrata

Net algal productivity at each site was assessed by measuring chlorophyll *a* accrual (a reflection of algal biomass) on artificial substrata placed monthly in each stream. Two types of substrata were used, plain unglazed ceramic tiles (10 cm x 10 cm) and identical tiles covered with grass carpet. The former simulated stones and the latter, bryophytes. Pairs of tiles (one of each type) were placed in metal tile holders and five pairs of holders were placed at various locations within the stream. Within each pair, one carpeted and one plain tile faced upstream (Fig. 2). Tiles were removed after two months as recommended by Biggs (1989), placed into plastic bags on ice in the field and transported back to Christchurch and frozen (-18°C) pending chlorophyll analysis. Sampling was conducted for 29 months, from May 1987 to September 1989.



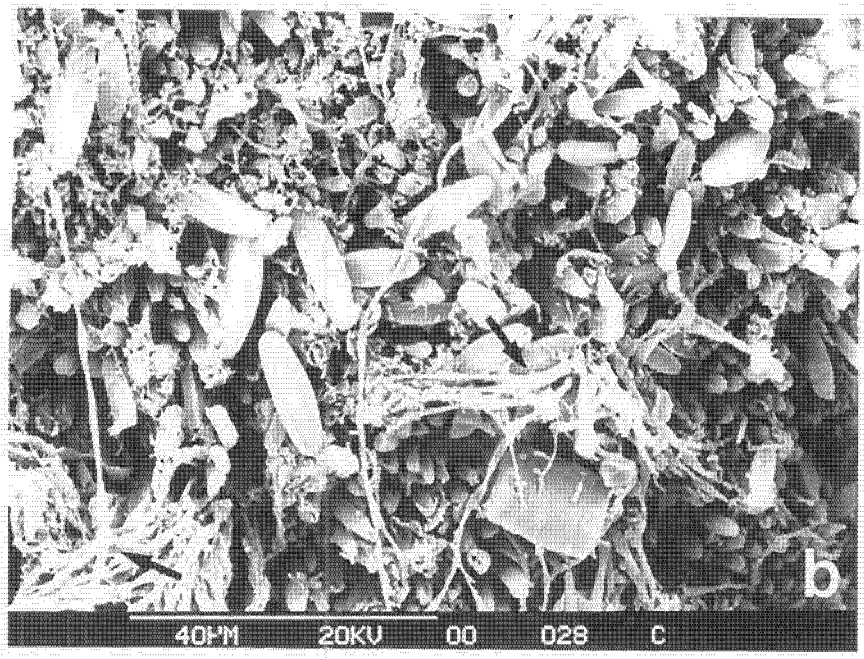
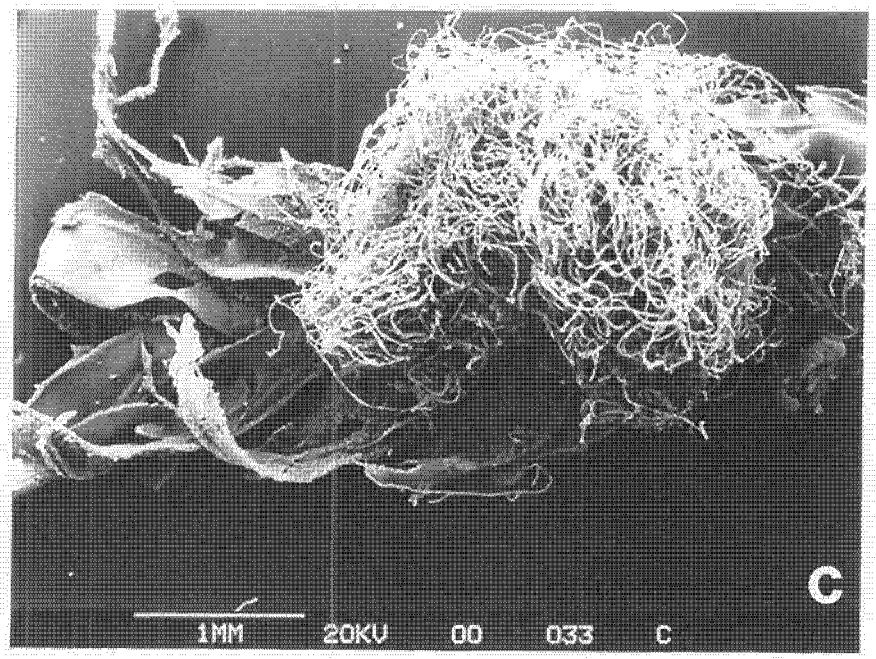


Fig. 1: Scanning electron micrographs of periphyton colonising selected bryophytes at Mouse Stream. Periphyton heavily colonised the basal stems of *Cratoneuropsis relaxa* (a) and was dominated by the diatoms *Navicula* and *Diatoma* and the blue green alga *Chamaesiphon*. Fungal hyphae (arrowed) were also evident (b). Blue-green algae (e.g., *Tolypothrix*) often colonised the adaxial surfaces of *Fissidens rigidulus* (c), the leaves of which were also heavily colonised by diatoms (d).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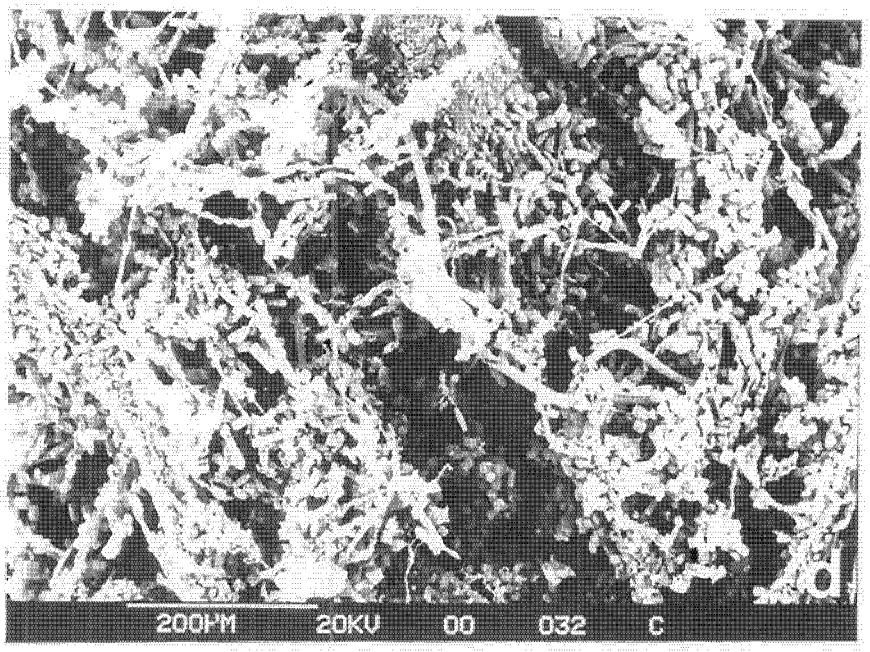
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Fig. 2: To assess periphyton accrual at each site, two types of artificial substrata were used. Plain unglazed ceramic tiles simulated rocks, and tiles covered with grass carpet simulated bryophytes. Two pairs of these tiles were placed in metal tile holders at each site with one plain and one carpeted tile in each pair facing upstream.

Chlorophyll analysis

Upon thawing, tiles were placed into Pyrex evaporating dishes (500 ml) and immersed in enough 90% ethanol to completely cover the tile. Dishes were then covered with a thin film (0.5 mm) of PVC plastic to prevent evaporative losses. Samples were analysed for chlorophyll *a* and phaeopigment following 10 min. boiling (Sartory & Grobbelaar 1984) and 2 hours incubation at 5 °C (Appendix 2). Extract volume was measured and a 5 ml subsample was removed and filtered (Whatman GFC) under vacuum. Absorbance at 665 nm and 750 nm (background) were read before and after acidification (0.1M HCl, 1h), using a Uvicon spectrophotometer (1 cm cells). Chlorophyll *a* and phaeopigment concentrations were calculated as described by Sartory & Grobbelaar (1984).

Trapped organic matter

Amounts of organic matter trapped on the grass carpet tiles placed in each stream for 2 months were determined each month from October 1987 to August 1989. Following chlorophyll *a* extraction, trapped organic matter was removed by hosing the carpets with high pressure water and scrubbing them with a stiff, nylon brush. This procedure was repeated twice, and all water and dislodged particulate matter (i.e., FPOM) was poured into a container through a sieve (53 µm mesh) on which all fine particulate matter collected. After being thoroughly stirred, UFPOM (<53 µm) in a subsample of the water in the container was collected on a pre-ashed Whatman GFC filter paper. All material retained by the sieve and the filters was dried (60°C, 48 h) and ashed in a muffle furnace (550°C, 12 h), and ash free dry weight (AFDW) was determined.

Statistical analysis

As the data were still non-normally distributed following $\log_{10}(x+1)$ transformation, non-parametric ANOVA (PROC NPAR1WAY, SAS 1988) was used to determine whether algal net productivity, and quantities of trapped FPOM and UFPOM differed between sites and substrates. Where significant differences occurred, the multiple range comparison test (Zar 1984) was used to determine which samples differed.

In order to assess temporal variability of algal production and biomass of trapped detritus, the coefficient of variation (CV) (Zar 1984) of each variable from each substrate type and site was calculated (data from all trips combined). The "predictability" of each variable (i.e., the percentage difference of each monthly data point from the long term average value) was then calculated. A non-parametric ANOVA was used to ascertain whether the magnitude of these percentage differences was related to substrate type or site.

Periphytic assemblages

The composition of periphytic assemblages was examined on five replicate tiles (6.25 cm^2) and equal sized pieces of grass carpet that were placed in plastic tile holders (5 cm x 20 cm) and exposed in each stream for two months from June to August 1988, and from December to February 1989. Tiles were fixed in the field in 2% gluteraldehyde in phosphate buffer (pH=7.4). Half the samples were prepared for scanning electron microscopy following post-fixing in OsO_4, dehydration in an ethanol/amyl acetate series and critical point drying (O'Brien and McCully 1981). Periphyton on the other tiles was removed by scraping with a razor blade and taxonomic composition assessed by light microscopy.

2. Benthic organic matter biomass

As part of the 18 month sampling programme conducted at each site (Chapter 2), organic matter was collected from riffles and bryophyte samples. This material was passed through nested sieves and separated into 4 size fractions (> 2mm, LPOM; 1-2 mm, CPOM; 0.5-1 mm, MPOM; 0.25-0.5 mm, FPOM). Samples of each size fraction were dried to constant weight (60°C, 48 h) and AFDW was determined following ashing in a muffle furnace (550°C, 12 h). Data were analysed as described above for algae.

RESULTS

Algal net productivity

Periphyton chlorophyll *a* content varied seasonally at both sites, with peaks in spring (October-November) each year. Chlorophyll *a* minima were observed in winter (June/July) at both sites (Fig 3). Significant differences in chlorophyll *a* content occurred between sites ($F= 223.7$, $p<0.0001$). Periphyton biomass was always higher at Mouse Stream than Tim's Creek; mean annual production x= 3.42 µg cm^{-2} at Mouse Stream, 0.56 µg cm^{-2} at Tim's Creek.

Carpeted tiles at Mouse Stream were often colonised extensively by periphyton which formed a thick coating over individual grass carpet "stems" (Figs 4a,b). Pigment analysis indicated that chlorophyll *a* values were always higher on carpeted tiles than plain ones ($F= 250.2$, $p<0.0001$), and mean annual biomass (as chlorophyll *a*) was almost 10 times greater on the former (3.11 µg cm^{-2}, Mouse Stream carpet; 0.32 µg cm^{-2}, Mouse Stream tiles; 0.50 µg cm^{-2} Tim's Creek carpet; 0.07 µg cm^{-2} Tim's Creek tiles). This reflects the greater available surface area of the grass carpet, and also possibly, the reduced flow between "stems", a condition allowing for greater algal biomass to accumulate before it is sloughed off.

Periphyton on grass carpets at Mouse Stream was dominated by flocculent masses of *Diatoma*. Other diatoms, including *Cymbella*, *Synedra*, *Navicula* and *Fragilaria*, and the filamentous green alga *Ulothrix* were also present at lower densities. Blue-green algae were not seen on artificial substrates.

Periphyton at Tim's Creek was less abundant than at Mouse Stream (Figs 4 c,d), and consisted primarily of the diatoms *Epithemia*, *Cocconeis* and *Cymbella*, and the filamentous blue-greens *Chamaesiphon* and *Lyngbya*. Large amounts of amorphous "slime" and associated bacteria were also commonly observed, especially on plain tiles placed at this site.

Temporal variability of algal net production, as indicated by coefficients of variation, were highest on plain tiles at Mouse Stream. The lowest CVs (i.e., the least variable production), were for plain tiles at Tim's Creek (Fig. 5). Average variation

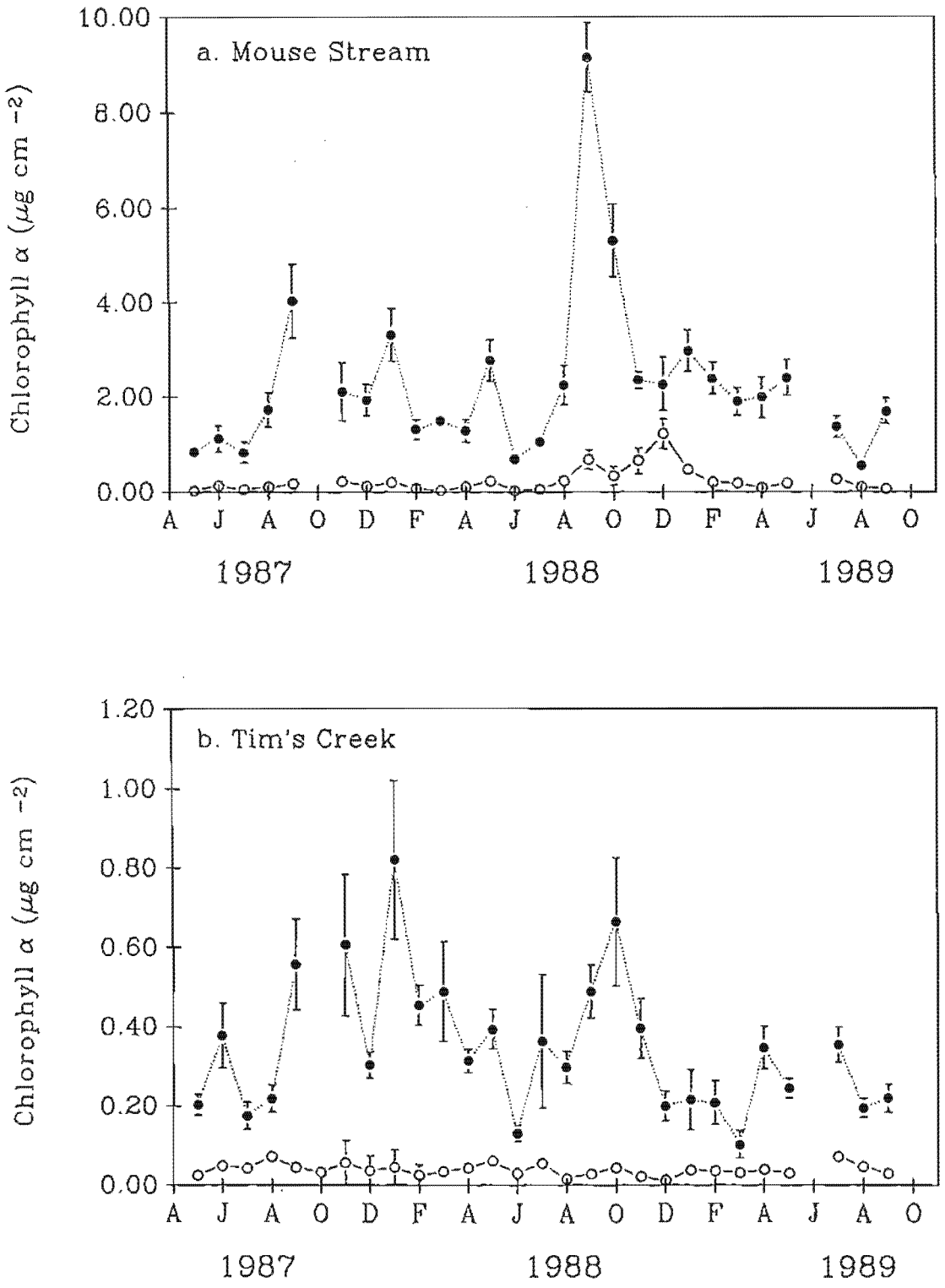
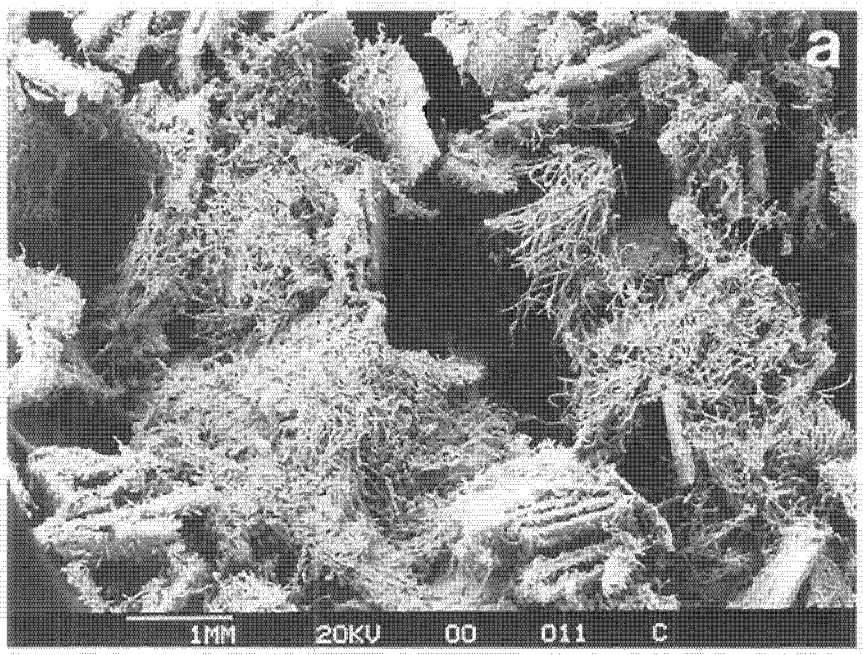


Fig. 3: Periphyton biomass (as chlorophyll *a*) on artificial substrates simulating rocks and byophytes at the two study sites from May 1987 to September 1989. a) Mouse stream; b) Tim's Creek. Open symbols plain tiles; closed symbols grass carpet covered tiles ($x \pm 1SE$, $n = 10$).



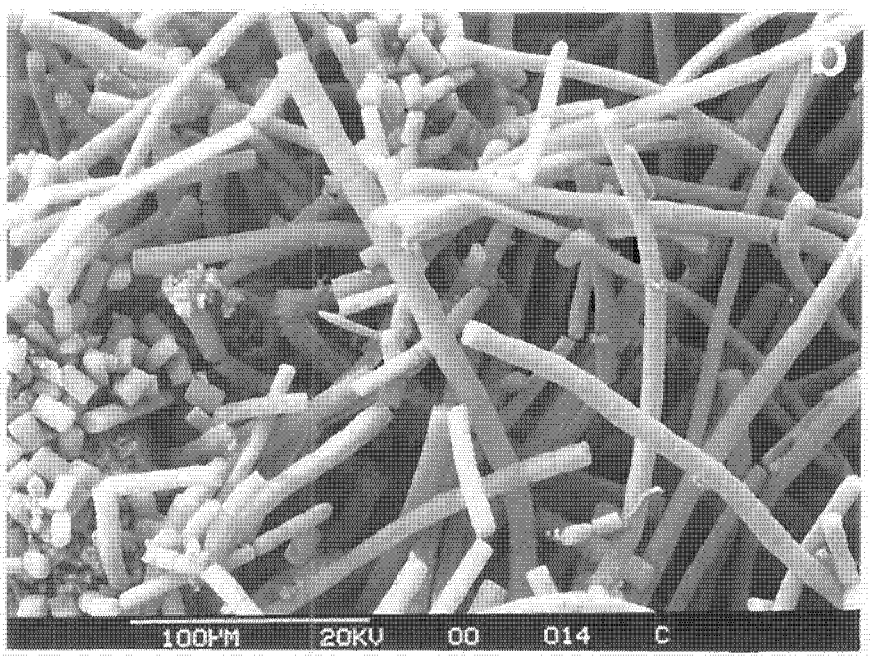
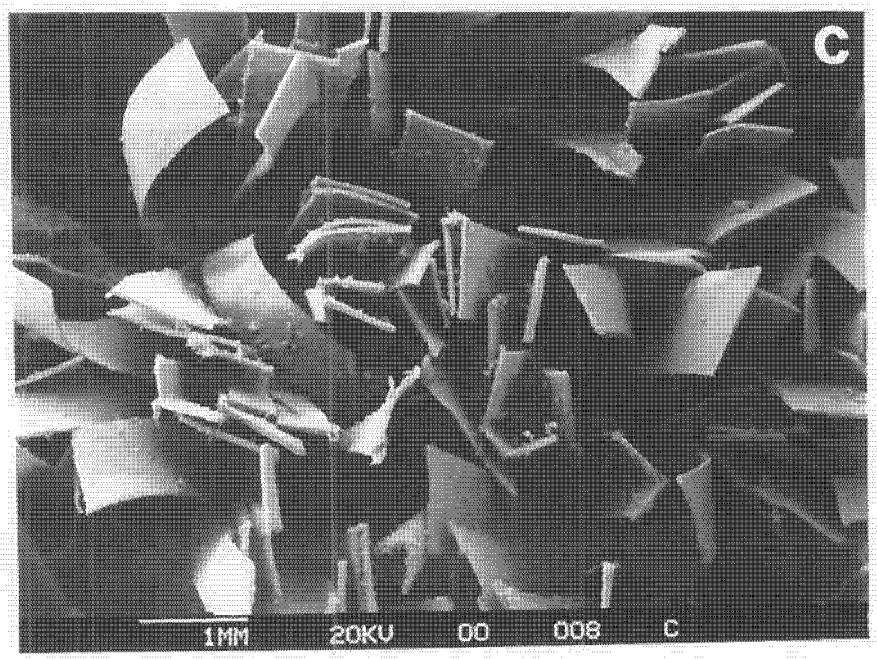


Fig. 4: Scanning electron micrographs showing periphyton colonizing grass carpet covered tiles at both sites. Carpet covered tiles at Mouse Stream were often extensively covered by large masses of the flocculent diatom *Diatoma* (a, b). Periphyton biomass at Tim's Creek was much less (c) and consisted mainly of *Gomphonema*, *Diatoma* and *Cocconeis* (d).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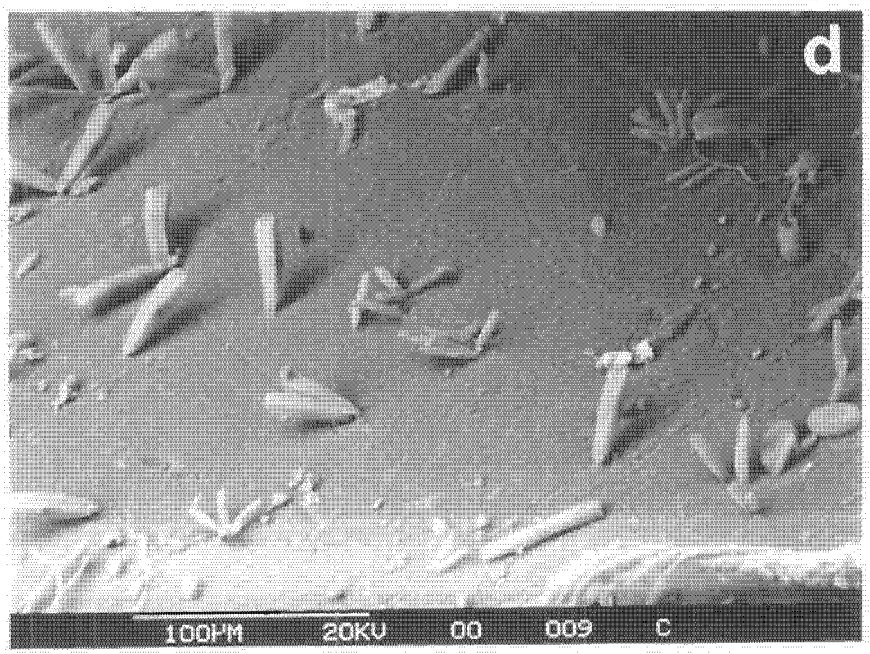
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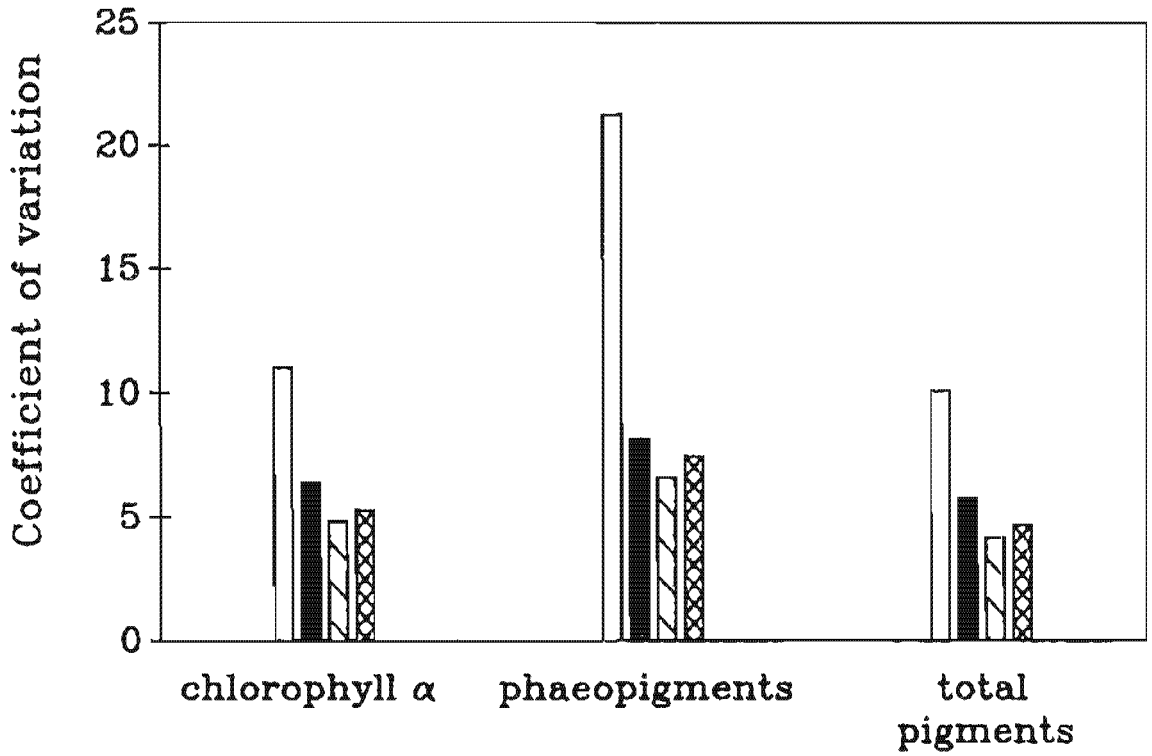

Fig. 5: Temporal variability of algal pigment concentration on plain and carpeted tiles at the two streams, expressed as the coefficient of variation calculated from the 29 monthly means. Open bars = plain tiles at Mouse Stream; closed bars = carpeted tiles at Mouse Stream; right hatching = plain tiles at Tim's Creek; Cross hatched bars = carpeted tiles at Tim's Creek.

between monthly sample means and the 23 month mean (i.e., the index of "predictability") for variables relating to algal productivity (chlorophyll *a*, phaeopigment and the two pigments combined) was significantly different between sites and substrate types (X^2= 31.34, 23.03, 66.98, respectively, $p<0.001$). Predictability was lowest on plain tiles from Mouse Stream, and was not significantly different among the other 3 substrate-site treatments although carpeted tiles from Tim's Creek always had the highest predictability.

Organic matter trapped by carpets

Grass carpet covered tiles at Tim's Creek trapped significantly more FPOM than carpeted tiles at Mouse Stream (x= 130 mg cm^{-2} at Mouse Stream, 320 mg cm^{-2} at Tim's Creek; Fig. 6 a) reflecting the greater amounts of detrital inputs to the forested site. Although organic matter weights varied significantly over time ($p<0.001$), no seasonal trend was evident (Figs 6 a,b). Amounts of FPOM trapped by carpets at Tim's Creek continued to increase throughout the study whereas amounts of FPOM present in carpets at Mouse Stream remained fairly constant during the study (Fig. 6a).

Carpeted tiles at both sites trapped similar quantities of UFPOM (Fig. 6b), with seasonal peaks in late winter-early spring in both 1987 and 1988. Biomass of trapped UFPOM was lowest in April-May each year.

Temporal variability for FPOM biomass trapped by carpeted tiles was greater at Mouse Stream than Tim's Creek (Fig. 7). Although carpeted tiles had a higher CV for UFPOM from Mouse Stream, the "predictability" of this variable did not differ between sites (Fig. 7).

Benthic organic matter

Significant temporal variations were found in quantities of organic matter taken in benthic samples from each habitat, but only in stony riffles was a seasonal pattern evident (Fig. 8). At both sites, samples taken from bryophytes contained more organic matter of each size fraction than did samples from riffles. However, bryophyte and riffle

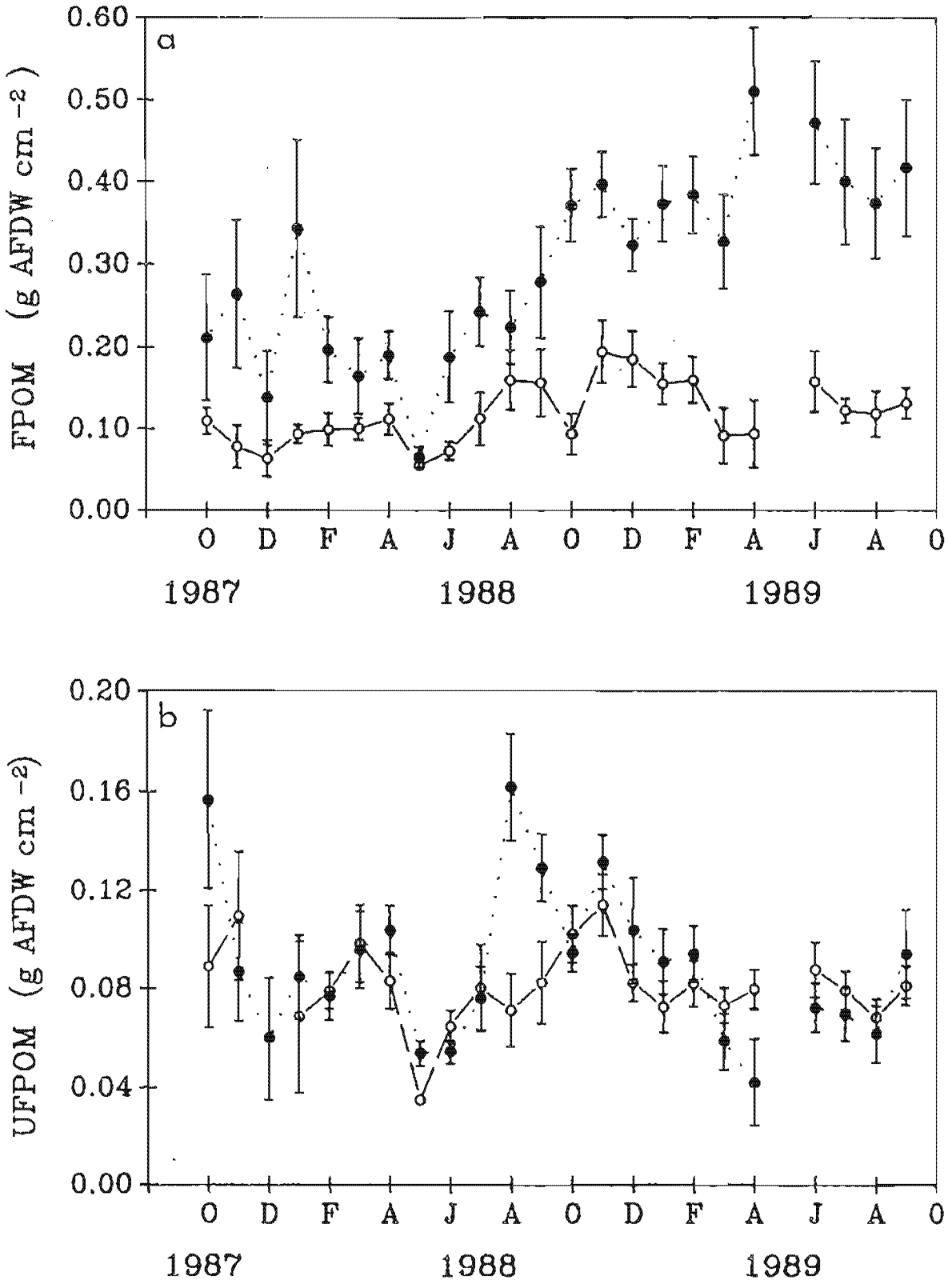

Fig. 6: Biomass of detrital material trapped by bryophyte simulating grass carpets at each site from October 1987 to September 1989. a = FPOM (>53 µm); b = UFPOM (<53 µm). Open Symbols = Mouse Stream; closed symbols = Tim's Creek (x ± 1 SE, n = 10).

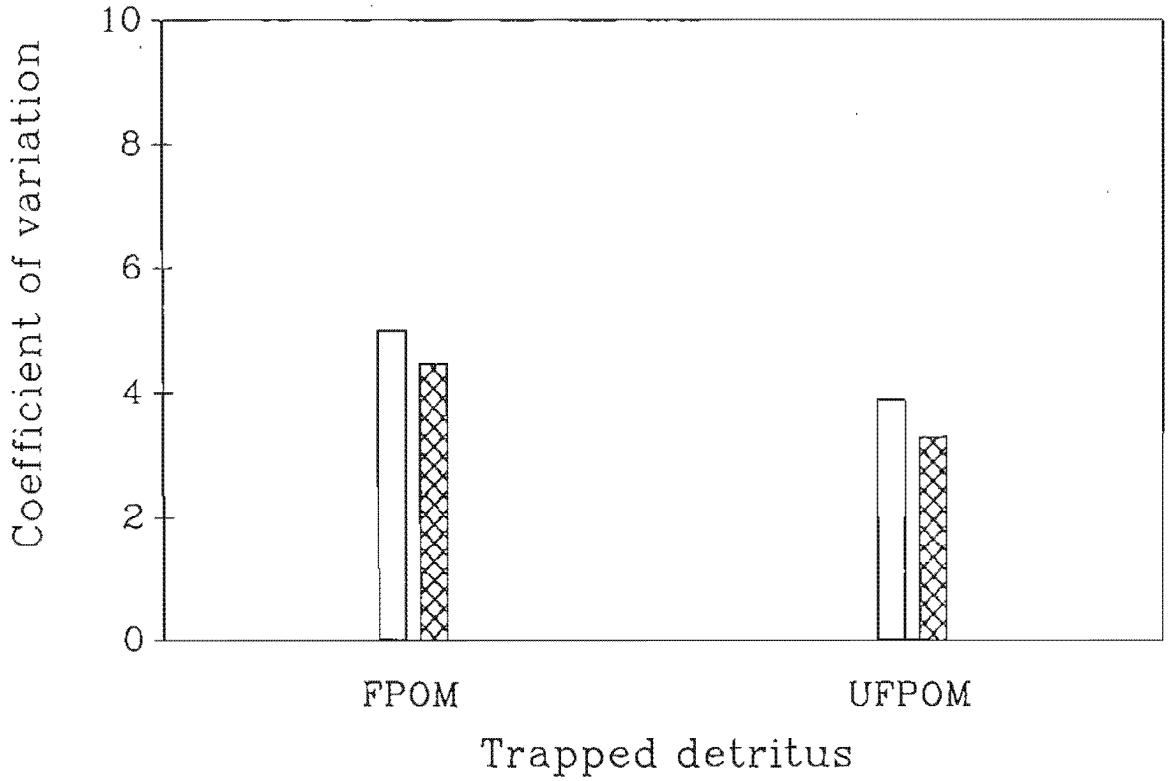

Fig. 7: Temporal variability of detritus (FPOM and UFPOM) trapped by carpeted tiles expressed as the coefficient of variation calculated from 29 monthly means. Open bars = Mouse Stream; hatched bars = Tim's Creek.

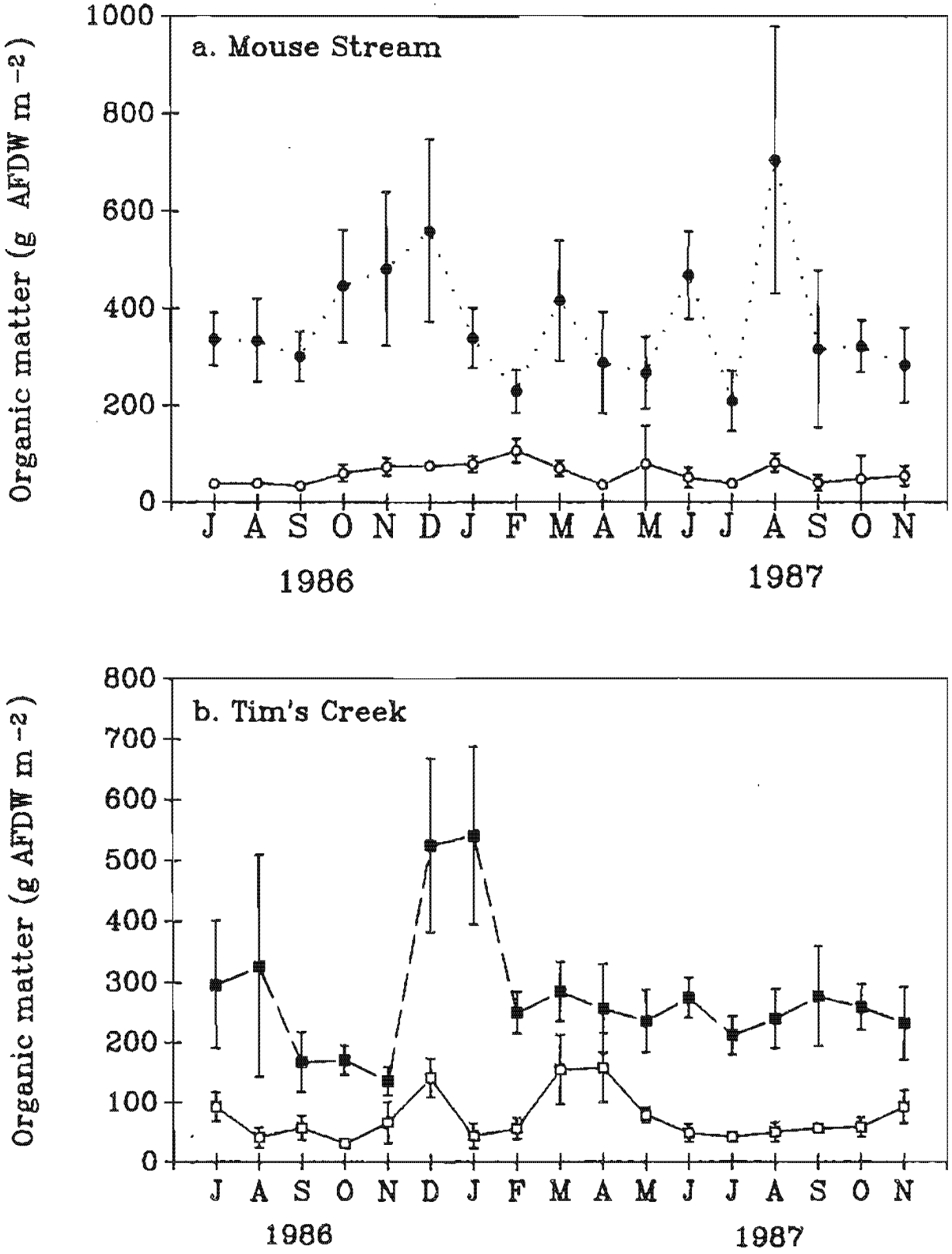

Fig. 8: Total organic matter collected monthly in riffle and bryophyte samples from at the two study streams, July 1986 to November 1987. a = Mouse Stream; b = Tim's Creek. Open symbols = riffles; closed symbols = bryophytes ($x \pm 1$ SE, n = 5).

samples from Mouse Stream contained similar quantities of organic matter to samples taken from the same habitats at Tim's Creek.

Temporal variability in the amount of organic matter collected from both habitats at Mouse Stream and Tim's Creek was greater in samples from riffles than from bryophytes (Fig. 9). Riffle samples from Tim's Creek were more variable than those from Mouse Stream for all size fractions except LPOM (Fig. 9). No comparable site differences were found for organic matter trapped by bryophytes.

DISCUSSION

Differences in the quantity of detritus trapped in stony riffles and by bryophytes and their grass-carpet analogues were found between the two study streams. These appeared to reflect differences in light regime and substrate stability. Net periphyton biomass production was higher at Mouse Stream over the course of the study although it varied considerably in time whereas at Tim's Creek it was lower but less seasonally variable.

Although current and substrate stability are known to influence algal biomass (Tett *et al.* 1978, Fisher *et al.* 1982, Scrimgeour *et al.* 1988, Biggs & Close 1989), the crustose, *Epithemia*-dominated community at Tim's Creek appeared to be less affected by substrate movement and scouring than the loosely adhering, flocculent *Diatoma*-dominated algal assemblage characteristic of Mouse Stream. Algae were consumed by invertebrates at both sites, and at Tim's Creek where algal standing crops were lower, they often made up to 10% of the gut contents of the cranefly *Limonia hudsoni* (Chapter 6).

In contrast to algal production, biomass of fine detritus within the stony stream bed and trapped by mosses was much greater at Tim's Creek than at Mouse Stream. Organic matter inputs to each stream were almost certainly greater at Tim's Creek, and in 1987 when some driftnet[1] sampling was undertaken, more particulate organic matter was in transport at Tim's Creek than Mouse Stream ($\bar{x}$= 0.793 g day^{-1} (dry weight) at Tim's Creek; 0.247 g day^{-1} at Mouse Stream: F= 17.8, $p<0.001$).

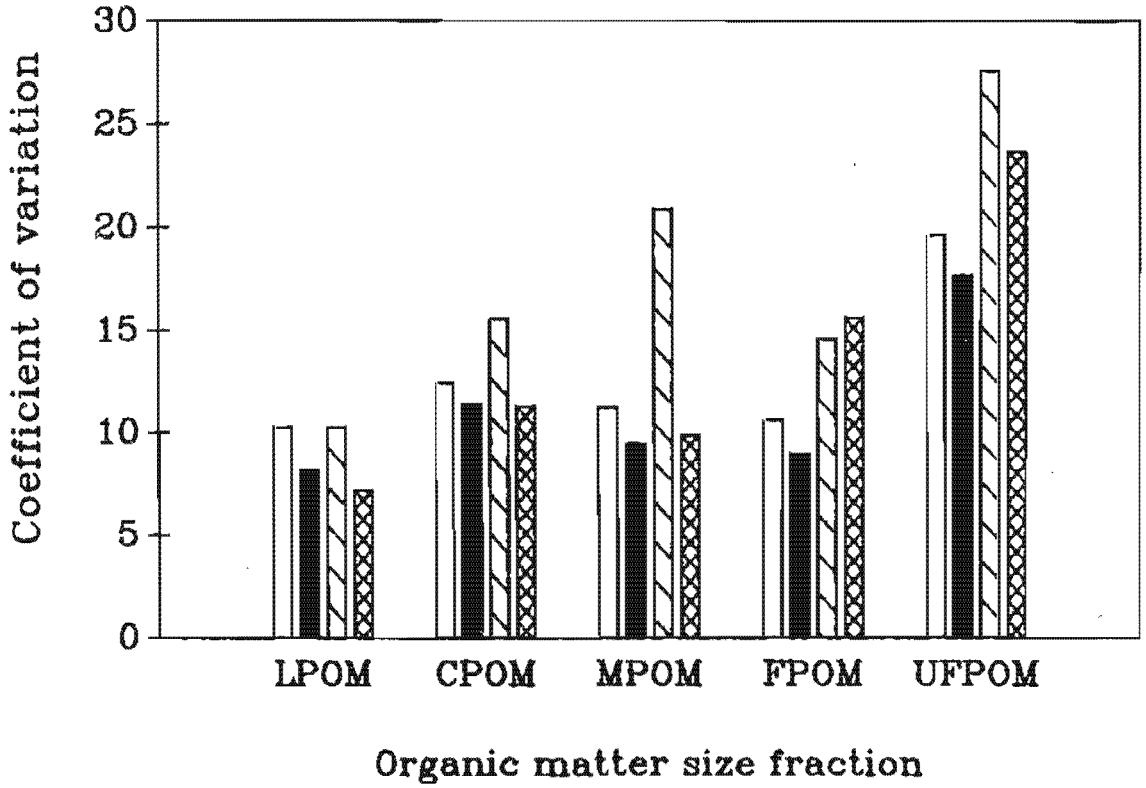

Fig. 9: Temporal variability of different size fractions of organic matter present in riffle and bryophyte samples from the two streams. Variability is expressed as the coefficient of variation, calculated from 17 monthly data. Open bars = riffles at Mouse Stream; shaded bars = bryophytes at Mouse Stream; Right hatched bars = riffles at Tim's Creek; cross hatched bars = bryophytes at Tim's Creek.

Although more FPOM probably entered Tim's Creek than Mouse Stream, bryophytes at each site trapped similar quantities of this material. This, however, reflects differences in bryophyte morphology. Stems of the dominant liverworts at Tim's Creek, *Plagiochila retrospectans* and *Hepatostolonophora paucistipula* were not as tightly packed as those of the mosses *Cratoneuropsis relaxa* and *Fissidens rigidulus* at Mouse Stream, and were consequently less efficient at trapping the greater quantities of fine particulate matter in transport at the former site. Differences in trapping efficiencies related to bryophyte morphology were also inferred by Smith-Cuffney (1987) and Cox (1988).

The biomass of fine organic matter trapped by bryophytes at both sites did not vary greatly with time in contrast to that in riffles, and therefore provided a predictable resource available to detrital feeding invertebrates.

Low light intensity in forested headwater streams can be expected to reduce autotrophic algal production and biomass but bryophyte biomass was similar at the two experimental sites. Indeed bryophytes form conspicuous growths on stable substrata in many New Zealand forested streams. They are typically shade adapted (Martin 1980, Martin & Churchill 1982) and some species have an outstanding ability to utilise very low incident light, as exemplified by those at extreme depths in lakes (e.g., at 130 m in Crater Lake, Oregon, USA (Hasler 1938), or under permanently ice-covered lakes in Antarctica (Korotokovich 1964, Light 1975, Light & Lewis-Smith 1976, Longton 1988).

Many rheophilous bryophytes are also characteristically red, black or dark green because of the presence of secondary pigments that prevent damage to chlorophyll and protein by UV light (Glime & Vitt 1984). Glime (1984) found that populations of *Fontinalis antipyretica* exposed to direct sunlight had more red pigments than those grown in the shade. Of the mosses found at Mouse Stream where

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[1]To assess quantities of organic matter inputs into each stream three replicate drift nets were placed in each stream at times of high (May 1987) and low stream discharge (June 1987). Nets were left for 24h, with material being removed at 12 h intervals from the nets.

shading of the streambed was minimal, *Bryum blandum* was red, and *Fissidens rigidulus* was dark green.

In addition to covering often large areas of exposed bedrock and other stable substrate materials in streams, bryophytes provide an important habitat for algal populations, and trap large quantities of fine detritus (Douglas 1958, Lindegaard *et al.* 1975, Johnson 1978, Maurer & Brusven 1983, Smith-Cuffney 1987). Mosses enhance autotrophic production by providing algae with a stable, high surface-area substrate for colonization, and possibly a minor source of dissolved organic carbon utilizable by them (See Chapter 6).

The commonly held assumption that autotrophy is unimportant in forested headwater streams (Fisher & Likens 1972, 1973, Vannote *et al.* 1980) was based, in part, on the belief that low light intensity severely restricts the development and production of autotrophic populations. An inferred consequence of this, is that low algal biomass is insufficient to support large populations of grazing invertebrates. Nevertheless, it is now appreciated that even if headwater streams are primarily dependent on allochthonous sources of energy, and have low periphyton standing crops, periphyton may nevertheless have a rapid turn-over and thus be capable of supporting high densities of invertebrates (McIntire 1973, Mayer & Likens 1987).

In contrast to many algae, aquatic bryophytes are not adversely affected by the low light intensities characteristic of forested headwater streams, and often form dense growths on stable substrata (Glime 1968, Craw 1976, Sheath *et al.* 1986). Although growth rates of bryophytes are low (Kelly & Whitton 1987), the plants are usually long-lived and consequently may have the potential to greatly affect stream energetics (Dawson 1973, Nalman 1983). By reducing currents within their matrices, and because they are highly stable "structures" in streams otherwise characterised by often extreme substratum movement, bryophytes not only provide a substratum for algal colonization and trap fine particles, but they also increase the "predictability" of these materials that represent significant food resources of invertebrates.

CONCLUSIONS

Bryophytes are a common feature of many first order, New Zealand alpine streams where they attain a high biomass even in shaded situations. They often trap large quantities of fine organic matter and consequently increase the retention of this material in streams where amounts of benthic organic matter can be low.

Bryophyte mimics also greatly enhanced algal biomass in each stream. This was a reflection of the enhanced greater surface area available for algal colonization and the reduction of water velocity within their matrices. A similar enhancement of algal biomass accrual is postulated to occur in real plants, again reflecting their increased surface area and reduction of water velocities within their matrices. By contributing small quantities of dissolved organic matter, either leached from bryophyte cells or trapped detritus and its associated microbial community, bryophytes may also enhance periphyton growth among these plants.

The production of algal biomass above the tree-line was higher than in the, but production was also more variable above the tree-line. Although this site was less flood prone, its dominant alga, *Diatoma*, formed large flocculent coatings over both bryophyte mimics and real plants, and was less resistant to the physical stresses imposed upon it by flooding than the tightly adhering, crustose *Epithemia* dominated communities that developed on artificial and natural substrata below the tree-line.

Variability of algal biomass on bryophyte mimics was also lower than its variability on substrata mimicing stones, again indicating (by implication) the importance of bryophytes in enabling algal populations to persist in streams where algal biomass is otherwise low.

CHAPTER EIGHT:

THE IMPORTANCE OF BRYOPHYTES IN THE TRAPPING OF ALLOCHTHONOUS LEAF LITTER

INTRODUCTION

The importance of allochthonous inputs to stream ecosystems is well known (e.g., Fisher & Likens 1972, 1973, Cummins 1974, Bird & Kaushik 1981), and decomposing riparian vegetation forms a dominant food source for many invertebrates (e.g., Cummins 1973, Hynes 1975, Anderson & Sedell 1979, Bird & Kaushik 1981). New Zealand streams, however, are often short and steep, and experience frequent heavy rainfall which flushes out allochthonous organic material. Fluctuations in water level can be great and substrate movement is often extensive (Winterbourn 1986, Winterbourn *et al.* 1988). Streambed instability reduces not only the density and diversity of benthic invertebrates (Winterbourn 1986, Graesser 1988, Scrimgeour *et al.* 1988), but also the amount of stored benthic organic matter (McCammon 1978, Graesser 1988, Winterbourn *et al.* 1988). This has been implicated in the apparent scarcity of shredding invertebrates in New Zealand streams (Rounick 1982, Rounick & Winterbourn 1982) and in the frequent occurrence of a common assemblage of collector-browsers that feed on stone surface organic layers (Cowie 1980, Rounick & Winterbourn 1982) and fine particulate detritus.

Retention of coarse particulate organic matter within a stream is dependent not only on hydrologic features such as discharge and flow variability, but also on substrate-related features (e.g., debris jams, rocks, riparian and aquatic vegetation) and geomorphological features (e.g., pools, riffles, waterfalls). Studies in North American streams have illustrated the often profound influence logs have on stream morphology (Keller & Swanson 1979, Keller & Tally 1979, Benke *et al.* 1985, Sedell *et al.* 1988) and how these form debris jams that increase within stream retention of organic matter (Bilby & Likens 1980, Bilby 1981, Speaker *et al.* 1984, Trotter 1990), although quantities of organic matter are often retained at depths into the substratum in streams without log jams (Metzler & Smock 1990).

A common feature of many turbulent headwater streams, both in New Zealand and elsewhere are extensive growths of aquatic bryophytes (e.g., Martin 1946, Glime 1968a, Dawson 1973, Naiman 1983, Slack & Glime 1985, Sheath *et al.* 1986, Craw 1976, Ormerod *et al.* 1987). They are capable of accumulating large quantities of detritus

leaves, which may also be trapped on emergent bryophytes in splash zones near the main channel.

The investigation reported here examined the retention characteristics of four small alpine streams to determine whether bryophytes increase the retention of introduced allochthonous organic matter.

STUDY SITES

Four streams were selected in Arthur's Pass National Park, and a 64 m stretch of each was chosen for study. The frequency of bryophyte cover was determined by recording substratum type and presence of bryophytes at 50 cm intervals along each stretch. Two streams were classed as "mossy", and two were categorised as "non-mossy" based on the frequency of occurrence of bryophytes (see below).

The "mossy" streams studied were the upper reach of Tim's Creek (Chapter 2) and Snow Creek, 2 km south-east of Arthur's Pass township (Fig. 1). Topography of both streams was steep and their channels consisted of a series of bryophyte-covered, bedrock waterfalls separated by riffles and deep pools. Streambed stability was assessed by the modified Pfankuch (1975) procedure (see Chapter 2). Modified Pfankuch ratings for Tim's Creek and Snow Creek were 32 and 22 respectively, indicating high streambed stability; nevertheless substrate movement within unstable riffle areas was evident. Bryophytes were recorded at 40% of the transect points along the stream.

The "non-mossy" streams were the lower reaches of Tim's Creek just above its confluence with the Bealey River, and Jack's Creek, 1 km north of Tim's Creek (Fig. 1). The lower reaches of Tim's Creek had a gentle gradient and the stream channel consisted of shallow riffles and long, non-turbulent runs. Streambed stability was medium-low (43), and some bank erosion was evident. Bryophytes occurred at only 15% of sampling points along the transect.

Jack's Creek was a much larger stream (up to 3m wide) with a series of boulders forming small waterfalls, separated by shallow, fast-flowing riffles and deeper pools. Channel gradient was intermediate between that of the lower and upper reaches of

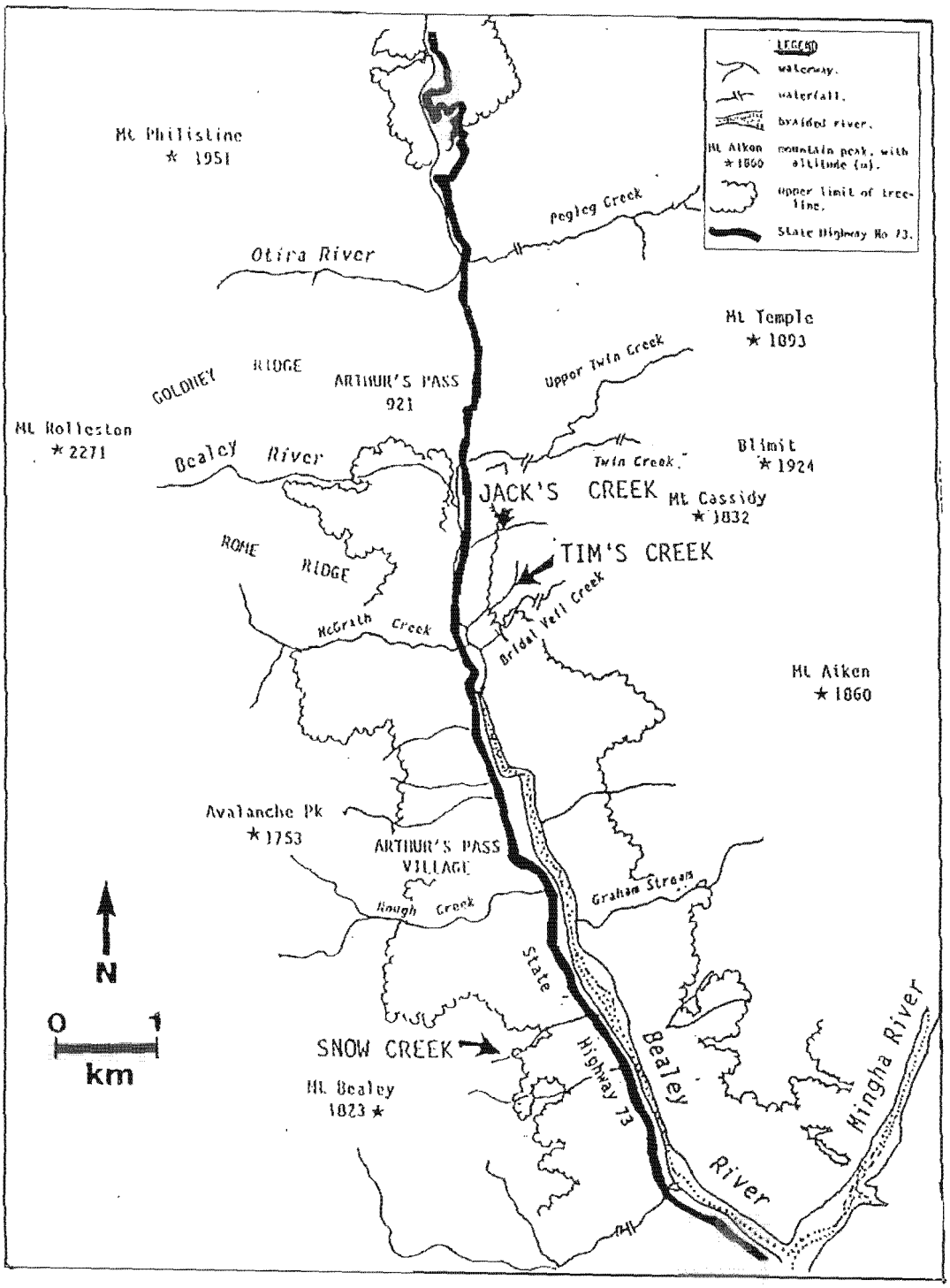


Fig. 1: Map showing the location of the four streams within Arthur's Pass National Park chosen for leaf retention studies. The "mossy" streams were the upper reaches of Tim's Creek, and Snow Creek, while the "non-mossy" streams were the lower reaches of Tim's Creek and Jack's Creek.

Tim's Creek. Streambed stability was low (50), few aquatic bryophytes were present, and there was considerable substrate heterogeneity and bank erosion. Bryophytes occurred at only 8% of sampling points along the transect.

MATERIALS AND METHODS

Retention "efficiency" of each stream was assessed by releasing 100 g dry weight of painted beech (*Nothofagus solandri* var *cliffortioides*) leaves and twigs at increasing distances from a downstream net (1 mm mesh). All litter had been collected from the forest floor at Arthur's Pass, and passed through nested sieves (mesh sizes 4 cm, 1 cm). Material retained on the 1cm mesh sieve was spray-painted with fluorescent paint (Dozzle ®); eight colours were used, leaves of each colour being released at a different distance from the net.

To assess whether painting leaves affected their transport characteristics by altering their buoyancy, three groups each of 100 leaves, and 20 twigs were spray painted and placed into separate Agee Jars of water (500 ml). Equal quantities of unpainted leaves and twigs served as controls. All jars were tightly capped and placed on a constantly shaking table for 48 h. The amount of material that had sunk after 24 and 48 h was measured.

Comparisons among streams

Samples of painted beech litter (100 g dry weight) were released at intervals of 2, 4, 8, 16, 24, 32, 48 and 64 meters upstream of a net. Three hours later, all leaves and twigs were removed from the net and grouped according to colour. Samples were air dried (60°C, 48 h) and weighed.

Water velocity in each stream was assessed by releasing a concentrated NaCl solution (250 ml) into the stream from each litter release point , and recording salinity every 5 s at the downstream net. The time it took for the peak salinity reading to be reached was used to calculate average flow velocity. All experiments were conducted

during periods of baseline discharge in each stream, the last rainfall having occurred 5 days or more prior to the experiments.

Within stream retention

In addition to examining rates of retention of leaf and twig material in streams with and without extensive bryophyte cover, I also examined sites of retention of leaves released within Tim's Creek. Following release of the coloured leaves from increasing distances upstream of the collecting net, I collecting these leaves from the various retention sites that prevented them from reaching the downstream net. These included pools, debris jams, and bryophyte-covered boulders in waterfalls and chutes (Figs 2 a-d).

Statistical analysis

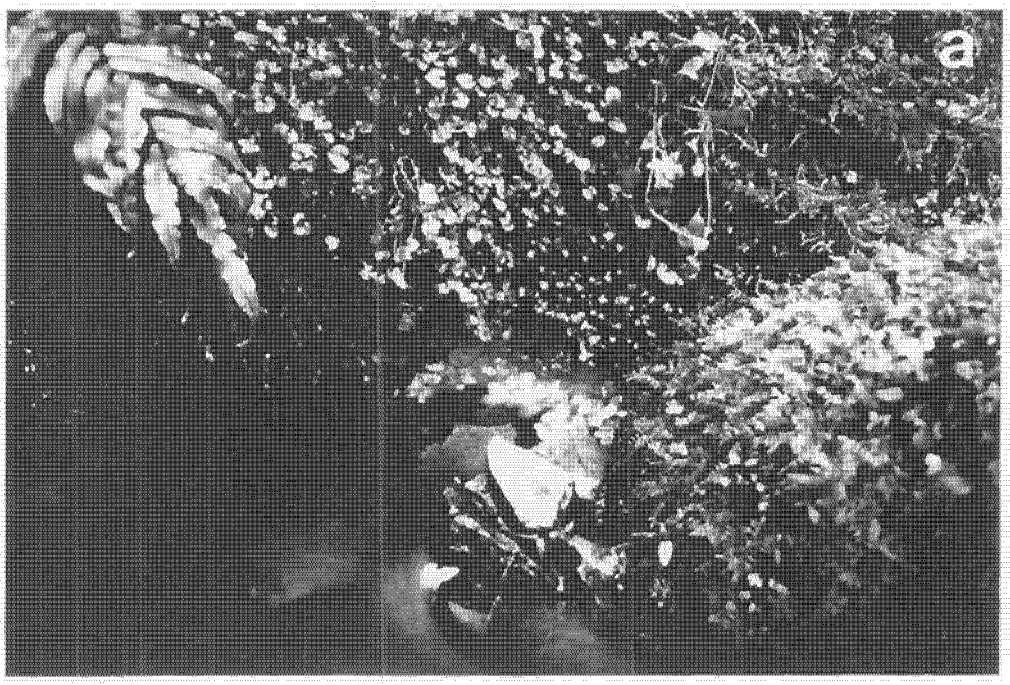
The relationship between biomass of leaves trapped in the downstream net and distance to the release point was determined by regression analysis following $\log_{10}(x+1)$ transformation of the leaf weight data. The slopes of the regression lines provided a measure of leaf retention in g m^{-1}. Differences in leaf retention, between streams was assessed by ANCOVA (PROC GLM; SAS 1988) with distance and site being the covariates.

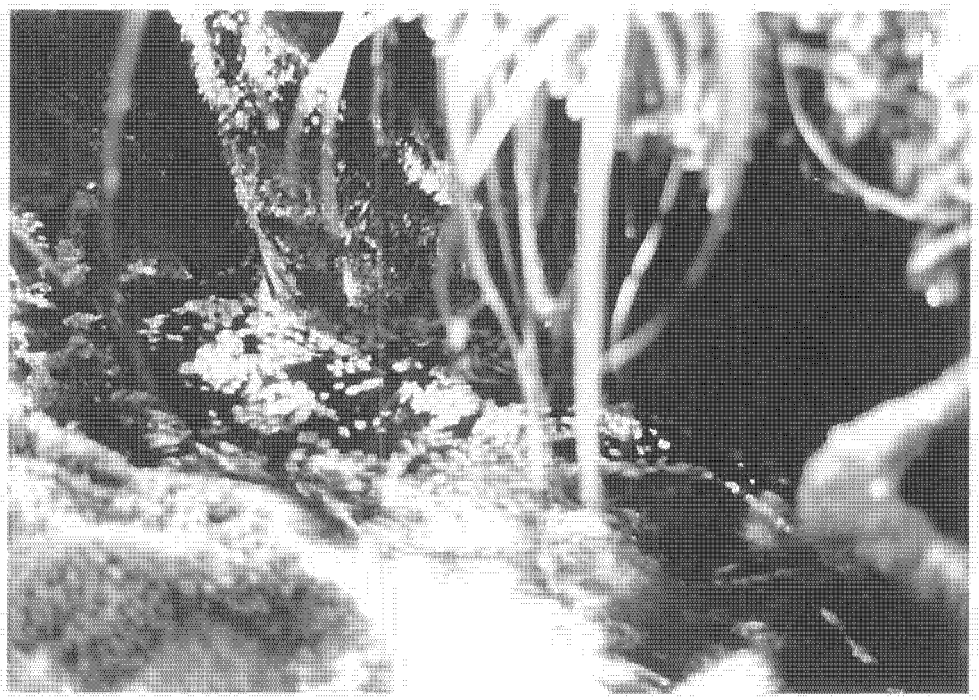
Determination of the retention efficiency of pools, debris jams and bryophyte-covered boulders in Tim's Creek was calculated by 2-WAY ANOVA (SAS, 1985) using retention feature and release distance as the independent variables.

RESULTS

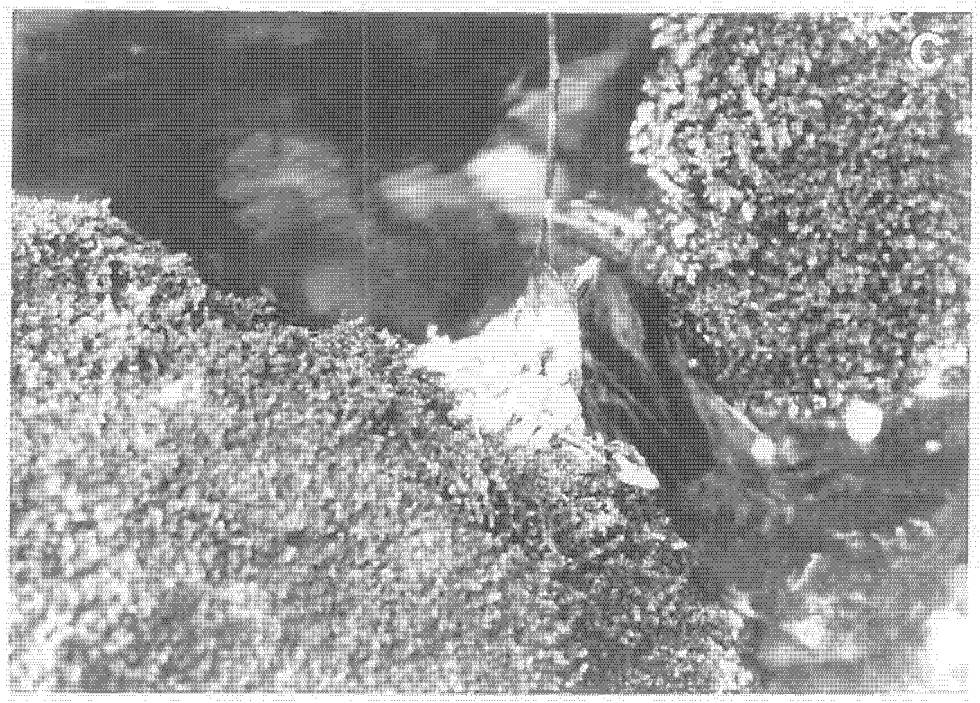
Effect of painting leaves.

No significant difference in the buoyancy of painted and control leaves was found even after 48 h when similar amounts of leaves became waterlogged and sank ($F= 0.24$, 24 h; $F= 0.96$, 48 h; $p>0.05$, Fig. 3a). Similarly, no significant differences in buoyancy of painted or control twigs were observed after 24 h ($F= 1.47$, $p>0.05$), whereas after





Figs 2a-d: Examples of retention features observed in Tim's Creek and other streams with luxuriant bryophyte growths; a, leaves trapped in still water at the water's margin; b, a deep pool where leaves remained circulating in eddies for the duration of a retention experiment (up to 24 h); c, a small debris jam formed by twigs between two boulders at Tim's Creek; d, bryophyte covered boulders forming a small waterfall.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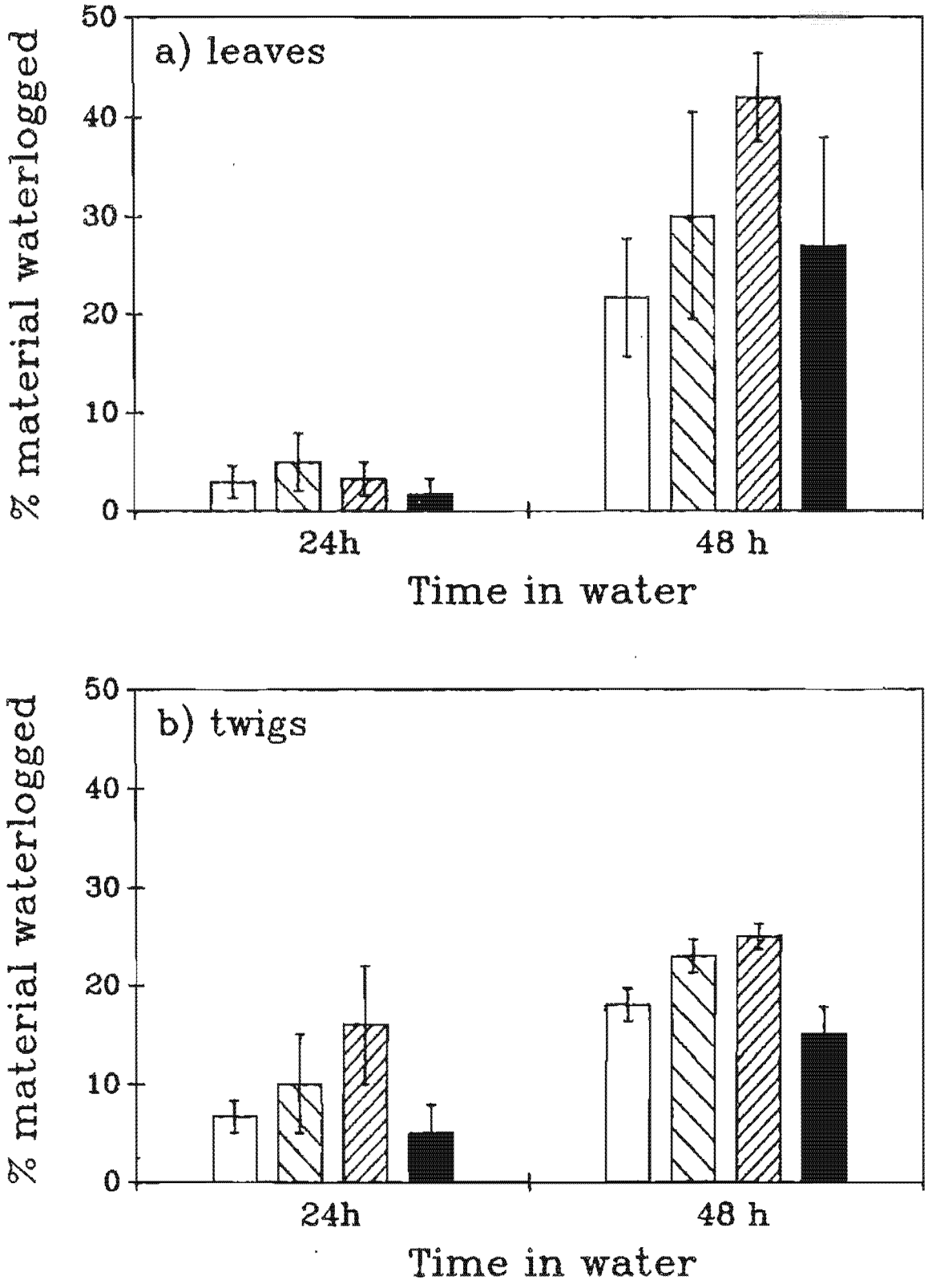

Fig. 3: The mean proportions of (a) beech leaves and (b) twigs that had sunk in five, continuously shaken jars after 24 and 48 hours ($\bar{x} \pm SE$, $n = 5$). Open and cross hatched bars represent three separate trials, each using a different colour of paint; closed bars represent control (unpainted) material.

48 h, slightly more painted than unpainted twigs had sunk ($F= 6.07$, $p<0.05$; Fig. 3b). I therefore concluded that the painting of beech leaves and twigs would have had little or no effect on their buoyancy characteristics in retention trials carried out in the streams.

Retention efficiencies of streams

Leaf Retention

Litter retention differed significantly between stream reaches (ANCOVA; $F= 2.96$, $p<0.05$). It was highest in Upper Tim's Creek, intermediate in Snow Creek, and lowest in Jacks Creek and Lower Tim's Creek (Fig. 4). The two "mossy" reaches therefore exhibited the greater degree of retentiveness.

Average reach flow velocity was higher in Snow Creek and Jacks Creek ($x= 0.27$ ms^{-1} and 0.25 ms^{-1}, respectively) than Tim's Creek and Lower Tim's Creek ($x= 0.13$ ms^{-1} and 0.16 ms^{-1}, respectively). Slopes of litter retention against distance travelled were therefore higher in the "mossy" than "non-mossy" streams of each velocity pair (Fig. 4). Thus, the presence of bryophytes enhanced retention of litter between streams of similar water velocity.

Retention rates (i.e., litter retention/water velocity) differed among reaches (ANCOVA; $F=8.78$, $p<0.05$) whereby rates were lowest in streams with highest average flow velocity (Fig. 5), and appeared largely unaffected by presence of bryophytes.

Retention sites

In Tim's Creek, bryophyte-covered boulders trapped significantly more material than either debris jams or pools, including bankside areas (2-WAY ANOVA; $F= 18.48$, $p<0.0001$; Fig. 6). Differences in the proportion of litter trapped in different retention sites were influenced by the stream topography, particularly the presence of pools close to release points. Thus, in releases from 32, 48 and 64 m, two large pools in these upstream areas trapped over 10% of leaves.

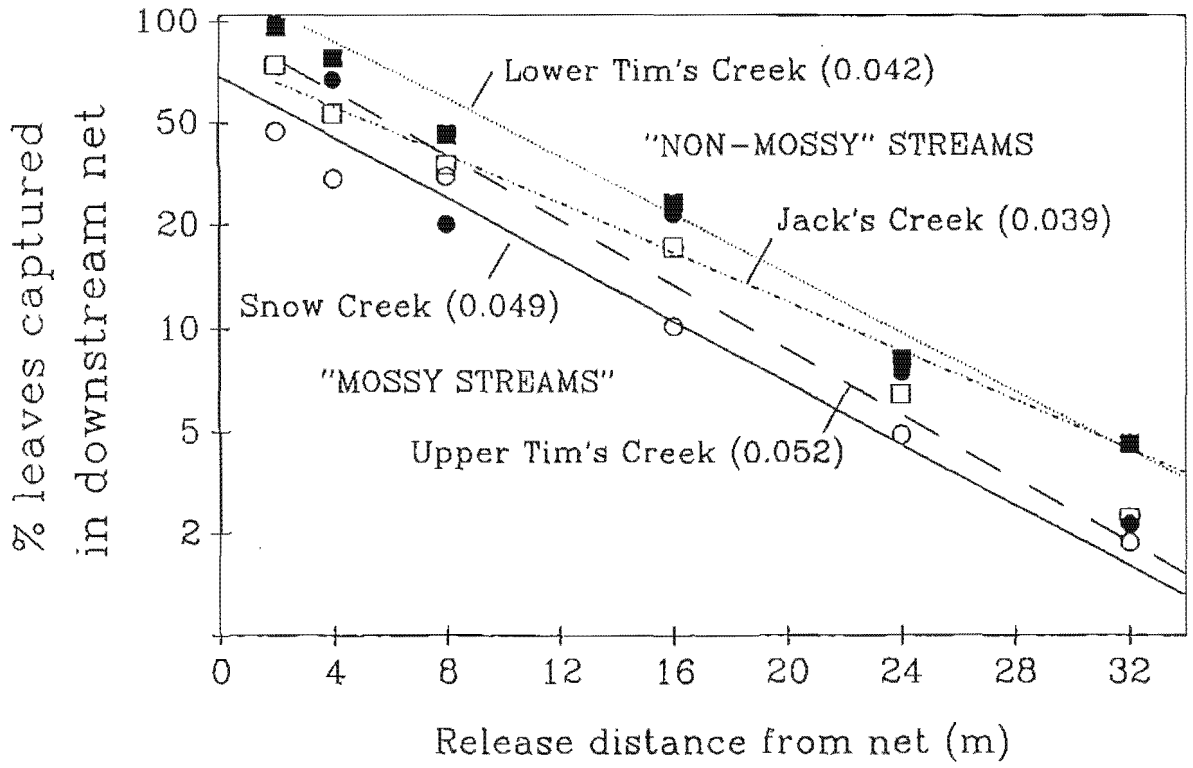

Fig. 4: The percentage of litter captured at increasing distances from a downstream collecting net in 4 stream reaches. Solid lines and open circles, = Snow Creek; dashed lines and open squares, = Tim's Creek; dotted lines and solid squares, = Lower Tim's Creek; dash-dot line and solid circles, = Jack's Creek. Slopes of the calculated regression line for each stream are given in parenthesis.

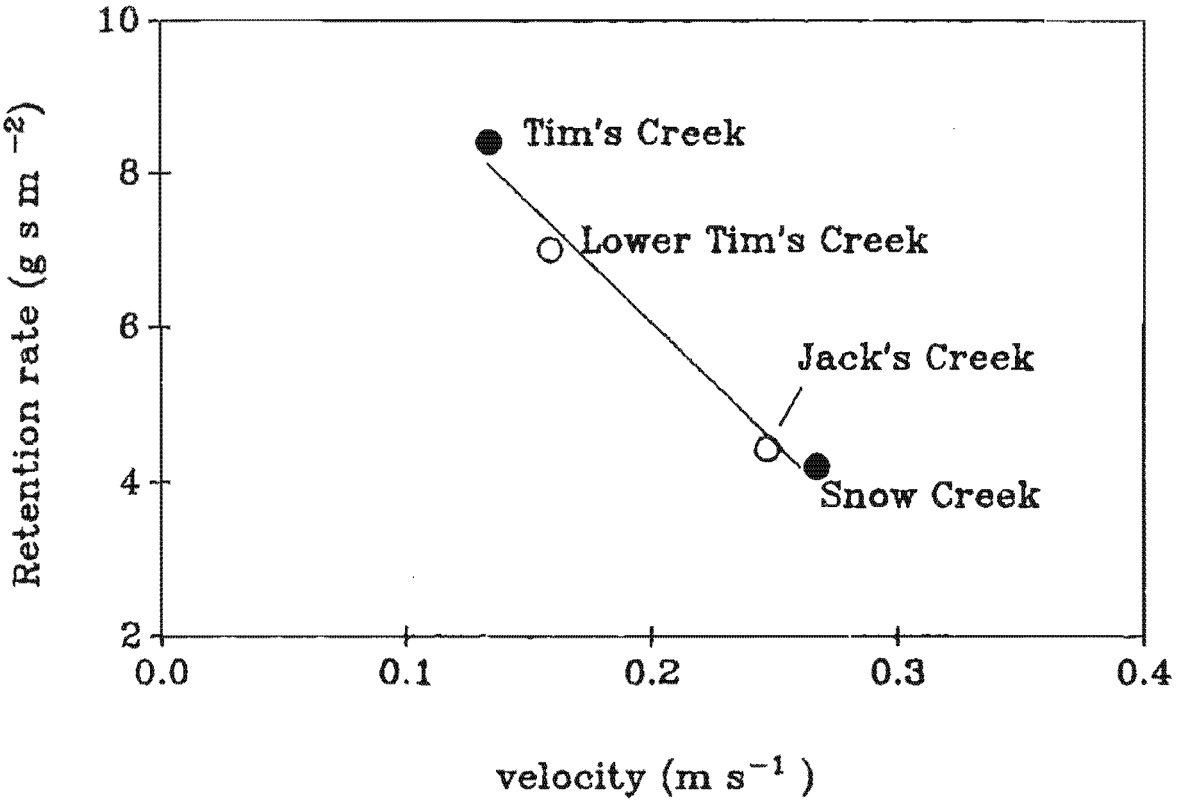

Fig. 5: Relationship between retention rate of beech leaves released into the 4 study streams upstream of a collecting net and the velocity of each stream. Faster flowing streams retained less material than slower streams, irrespective of the presence of bryophytes. Open circles, "non-mossy" streams; closed circles, "mossy" streams.

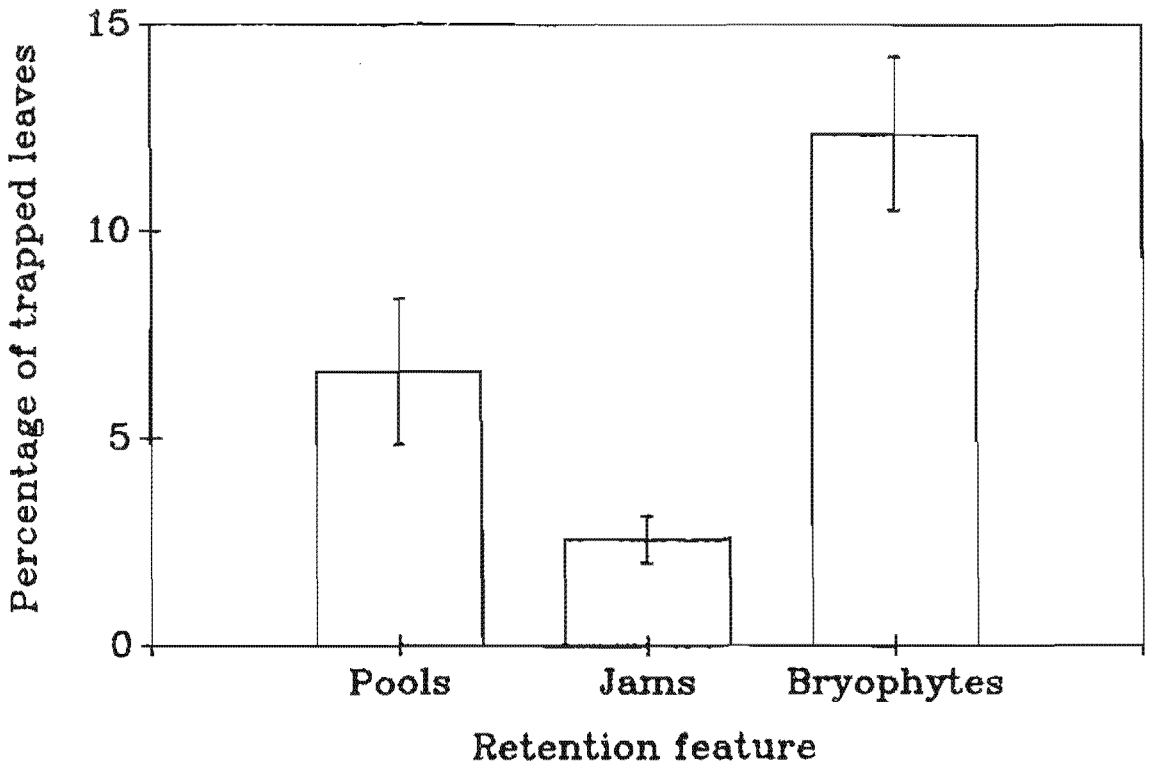

Fig. 6: Percentage of material trapped in pools, debris jams and byrophytes in a 64 m reach at Tim's Creek ($x \pm 1SE$, $n = 8$).

DISCUSSION

Entrapment of leaves within a stream depends upon the probability of leaves encountering an obstacle and on the hydrologic conditions around that obstacle. While the processes of retention and dislodgement of leaves from obstacles has been viewed as being highly stochastic (Young *et al.* 1978), previous studies have highlighted a number of predictable patterns (e.g. Speaker *et al.* 1984, 1988, Trotter 1990). In general, riffles are more retentive than pools regardless of substrate type, and substrates at a stream's margin are more efficient at trapping material than those in the main channel. Current velocity also influences the retention capacities of streams, with areas of faster current being less retentive (Speaker *et al.* 1984).

The presence of large organic debris (log jams) can also have a profound influence on stream hydrological processes (Keller & Swanson 1979, Keller & Tally 1979) and on the retention of small fractions of organic matter (Speaker *et al.* 1984, 1988). Strong linkages are postulated to exist between a stream and its surrounding valley catchment (Hynes 1975), and indeed biomass of benthic organic matter and densities of shredding invertebrates in headwater streams draining successional Aspen forests in the southern Rockies are less than in streams draining climax conifer forests (Molles 1982). Furthermore, this was illustrated experimentally in three second-order, New-Mexico (U.S.A), streams by the addition of wood to naturally unstable streams flowing through successional Aspen forest (Trotter 1990). This addition increased retention of introduced organic matter and increased channel stability by increasing channel morphology and deflecting water movement into eddies and backwaters.

An important feature of forest climax streams is the presence of logs on their beds and the subsequent formation of debris jams. These not only stabilise gravel beds and create energy dissipating steps within the stream (Heede 1972), but also change stream morphology and create depositional areas for benthic organic matter storage (Keller & Swanson 1979, Keller & Tally 1979, Benke *et al.* 1985, Sedell *et al.* 1988). Smaller sticks and wood (<10cm in diameter) have also been reported to greatly enhance leaf retention in streams, despite their being an apparently minor component of channel

structure (Speaker *et al.* 1984), but little attention has been paid to the role of bryophytes in this regard.

Many New Zealand headwater streams contain little wood and possess poor detrital retention characteristics (Winterbourn *et al.* 1981). Furthermore, large losses of CPOM are frequently associated with flood events (Winterbourn 1976). However, where extensive growths of aquatic bryophytes occur in New Zealand streams they are able to influence their retention characteristics. The "mossy" streams considered in my study were more retentive than the "non-mossy" ones, but the retention rates of leaves and twigs decreased as flow increased.

The importance of bryophytes as specific retention structures was clear in Upper Tim's Creek where they trapped more painted leaf and twig material than did boulders and pools. Furthermore, many non-painted beech leaves were observed to have been trapped by bryophytes in both Upper Tim's Creek and Snow Creek during times of low flow throughout the duration of the experimental study.

By trapping leaves, bryophytes make food materials available for shredders which otherwise might be confined to debris jams or pools or be unable to colonize a stream. In Tim's Creek, relatively high densities of the leaf and wood shredders *Zelandopsyche ingens* and *Austroperla cyrene* were found on bryophyte mats and gut content analysis indicated that they had ingested fragments of beech leaf as well as living bryophytes and accumulated detritus (Chapter 6).

CONCLUSIONS

Although many North American stream studies have emphasised the importance of allochthonous material in stream energy flows and in altering their retention characteristics, it is evident that autotrophic components of some small headwater New Zealand streams can also influence storage and retention of allochthonously produced material. In addition to their role as habitat, food, and shelter from currents, bryophytes therefore provide potentially important sites for litter retention and shredder feeding activity.

CHAPTER NINE:

GENERAL DISCUSSION

While conducting field work for this study, I quickly became aware of the often profound influence precipitation has on the landscape, especially the watercourses (Figs 1-4). Over 70% of my field trips were during periods of rain, and during 1987 there were two "100 year floods" within months of each other. Even in the headwater streams I studied, extensive streambed movement had occurred. Indeed, losses of experimental substrata at Tim's Creek on three occasions attest to the often violent disruptive force that water has even in small streams.

It is apparent, however, that despite extensive substratum movement, bryophytes growing on bedrock are little affected by flooding, and were virtually never washed away. In fact, loss of bryophytes was observed only once, at Mouse Stream during the second "100 year flood" of 1987 in September. At that time, an ice dam in the upper Otira Valley was thought to have suddenly collapsed, releasing a vary large quantity of water. This deluge not only washed away extensive scree and moraine deposits in the upper valley and destroyed a foot bridge (normally 2m above low flow; Fig. 5) over the Otira River, but deposited large quantities of rubble that smothered bryophyte covered boulders in the lower reaches of Mouse Stream.

Nevertheless, flooding of such magnitude is apparently "rare", and for many benthic invertebrates, bryophytes provide a stable habitat in streams where substratum instability and variable discharge are common.

Specific modes of bryophyte colonization by invertebrates are poorly known. However, in line with Sheldon's (1984) molecular diffusion model it seems likely that individuals colonize empty spaces until their numbers reach carrying capacity. A bryophyte mat may primarily receive individuals from the drift or through oviposition by adult insects.

Habitat selection by some taxa may reflect a morphological inability to survive in unstable riffles. For example, larvae of the cranefly *Limonia hudsoni*, tardigrades, nematodes, copepods and rotifers appear to be morphologically and behaviourally unable to dwell amongst constantly moving gravel and cobble substrates; however they are abundant among bryophytes. There they are able to burrow into, or live on, the plant which protects them from extremes of water and substratum movement and in some cases (e.g., *L. hudsoni*) provides them directly with food. In contrast, bryophytes may provide unsuitable habitat for some invertebrates that arrive by drift, perhaps because morphological constraints prevent them from moving amongst the plant stems. This is likely to explain the absence of *Deleatidium* and *Stenoperla prasina* larvae.

Other invertebrates may be capable of colonizing and living in riffles and amongst bryophytes but one or another may provide them with superior shelter or food resources. Thus, several stonefly and caddisfly species occur in both habitats although *Zelandoperla* sp., *Acroperla spiniger* and *Zelolessica cheira* dwell primarily amongst bryophytes, whereas *Austroperla cyrene* and *Oeconesus similis* are more common in riffles.

The main group of invertebrates that colonize bryophytes principally through oviposition is undoubtedly the Chironomidae. The importance of this mechanism for colonizing bryophytes has long been known (e.g., Alexander 1920, Byers 1961, Glime 1968b, Gerson 1972) and the high densities of chironomid larvae I observed attest to its significance. Although oviposition may be restricted to plants at the air-water interface, subsequent dispersion of newly hatched larvae can be expected to result in colonization of completely submerged plants. This senario is consistent with that advanced by Winterbourn (1990) for explaining the colonization of algal patches by species of Chironomidae in a South Island montane stream.

Following the initial colonization phase animals must "decide" whether to stay, or leave. Although specific reasons for immigration to and emigration from habitats by individuals are largely unknown (Sheldon 1984), some taxa are known to actively cue into habitats offering abundant food resources (e.g., McAuliffe 1983). I have shown (Chapter 5) as have others (e.g., Douglas 1958, Johnson 1978, McKenzie-Smith 1987) that the biomass and density of algal and detrital patches can be greatly enhanced by the presence of bryophytes. Thus larvae of chironomids, *Zelandoperla*, *Acroperla spiniger* and other invertebrates including some nematodes, tardigrades and copepods colonize bryophytes and utilise these abundant foods.

Other taxa, for example *Zelolessica cheira* and some chironomid species, utilise bryophytes as food and as a material from which to construct cases and retreats (Chapter 3, Appendix 4). Bryophytes represent a permanent, accessible and easily chewed material from which cases can be made, in contrast to the often tough, lignified leaf litter that occurs less predictably in these streams.

Taxa whose morphology appears to exclude them from riffles (e.g., *Limonia hudsoni*, tardigrades, rotifers and some nematodes), rely on bryophytes as shelter and they may have been faced with strong selective pressure to consume either trapped algae, detritus, or the bryophytes themselves. Bryophagy has previously been reported for a few aquatic taxa (e.g., tipulid larvae, Alexander 1920; tardigrades, Morgan & King, 1976; nematodes, Maslen 1981; and larvae of a stonefly and caddisfly, Mutch & Prichard, 1984a,b) and was observed in a small proportion of moss dwelling taxa considered in this study (Chapter 6).

The considerable degree of success attained by numerous invertebrate species in colonizing aquatic bryophytes is indicated by the high densities they can attain. One result of such enhanced invertebrate densities is an increase in the amount of prey potentially available to other consumers. Studies of bryophytes in Ireland (Frost 1939, 1942, 1945), and in North America (Maurer & Brusven 1983, Brusven *et al.* 1990) have demonstrated the importance of these plants to many insect taxa that are consumed by fish. The first order alpine streams I studied lacked fish, however, but swarms of adult chironomids and empidids whose immature stages inhabit bryophyte mats are a potentially important food source for avian predators.

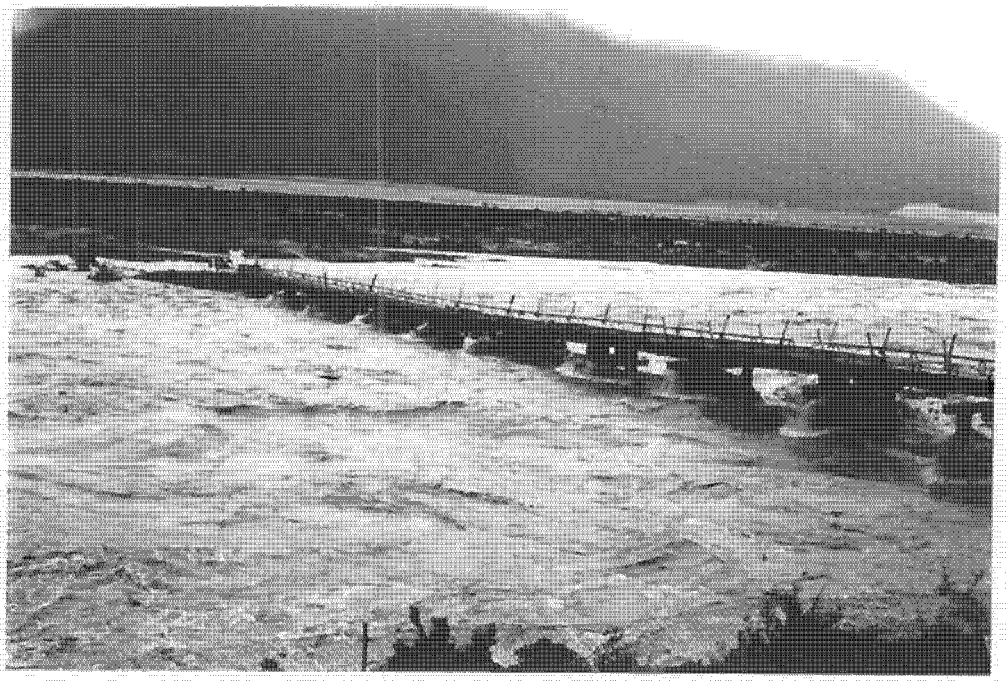

Fig. 1: The Waimakariri River in flood at the Mt. White bridge, 25 km. east of Arthur's Pass township, during heavy rains in September 1987. This bridge, normally 2 meters above the water, was closed untill the flood waters subsided. (Photo courtesy of Arthur's Pass National Park (APNP)).

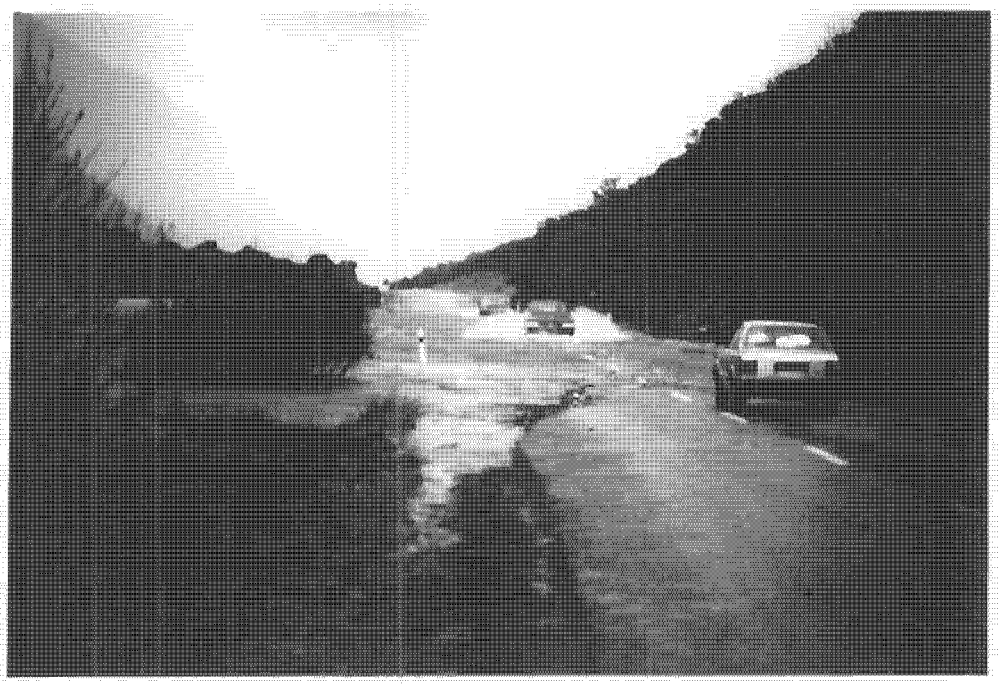

Fig. 2: Lake Misery, formed from lateral moraine from the old Otira Valley Glacier, fills from a small stream and runoff from its surrounding catchment, and usually drains into the Otira River as water percolates through the moraine deposites. At times of heavy rainfall (e.g., during the September 1987 flood), it often overflows and covers State Highway 73, four meters above. (Photo courtesy of APNP).

Fig. 3: Flash floods are a feature of many of the waterways in the Arthur's Pass region. Here the road bridge over the Otira River was washed out when 225mm of rain fell in 12 hours in December 1979. (Photo courtesy of APNP).

Fig. 4: High rainfall and flooding result in extensive substratum movement in streams. Here State Highway 73 lies beneath 4 meters of rubble at Reid Falls. This rubble was brought down from Candy's Creek, 100m from here, during high rainfall in September 1987, and consequently blocked the road. (Photo courtesy APNP).

Fig. 5: High water discharge has profound effects even in a catchment's upper reaches. This footbridge, over the upper Otira River some 600m from its source, was washed away without trace in September 1987 as a result of heavy rainfall, and the possible catastrophic collapse of an ice dam in the upper valley. (Photo courtesy APNP).

Pipits, (*Anthus novaeseelandiae*), Yellowheads (*Mohua ochrocephala*) and Rock Wrens (*Xenicus gilviventris*)) all consume adult aquatic insects, and I observed the latter feeding on swarms of adult chironomids and emergent stoneflies (apparently a species of *Zelandoperla*) on the river banks.

In the Otira Valley, and in other valleys of Arthurs Pass National Park including those of the Upper Waimakariri, Hawden and Mingha, small populations of the now rare Blue Duck (*Hymenolaimus malacorhynchus*) also occur. The diet of this bird consists largely of aquatic insect larvae (Kear & Burton, 1971, Williams 1985), although the fruits of *Coprosma* spp. and other alpine shrubs are taken when in season (Harding 1990, personal observations). Detailed feeding studies of Blue Duck have only been made in the North Island, notably in the Manganui-a-te-Ao where birds feed mainly on caddisfly, stonefly and mayfly larvae (Kevin Collier, pers. comm.). Blue Duck faecal material I examined from the Otira River also consisted mainly of sclerotised remains of aquatic insects which the birds dislodge from rocks with their beaks while feeding.

Moss fragments observed in the faeces of some individuals (Kear & Burton 1971) may have been accidentally ingested while the birds were feeding around moss covered boulders, and I have observed both adult and juvenile Blue Ducks consuming adult chironomids and tipulids that were swarming around bryophyte covered boulders.

Finally, at Tim's Creek, many spiders construct low-lying webs across the stream, especially close to bryophyte covered waterfalls and chutes. These webs catch adult flying insects, including chironomids, blackflies (*Austrosimulium ungulatum*) and tipulids (*Limonia* spp.), all of which are associated with bryophytes in their aquatic phases.

The presence of many small larval insects amongst mosses observed in my study and by others (e.g., Percival & Whitehead 1929, 1930, Hynes 1961, Lillehammer 1966, Egglishaw 1969, Stern & Stern 1969, Lindegaard *et al.* 1975, Thorup & Lindegaard 1977, McKenzie-Smith 1987, Smith-Cuffney 1987) indicate that bryophytes act as important nursery areas in streams. They may also serve as refugia for invertebrates during floods and subsequently provide an important source of recolonists following catastrophic flood events (Townsend 1989).

Finally, because of their physiological and ecological features, the roles played by bryophytes in ecosystems can be of more than academic interest. The simple morphology of bryophytes, which have only a rudimentary cuticle and no root system, means that all mineral uptake comes from the water, rather than the substratum. Bryophytes have a very high cation-exchange-capacity, and this enables rapid, yet passive (i.e., abiotic) extracellular cation uptake to occur (Brown 1984). Furthermore, chemical analysis of aquatic bryophytes has shown that they may become significantly enriched with heavy metals when growing in contaminated water (e.g., Burton and Peterson 1979, Say *et al.* 1981, Whitton *et al.* 1982, Satake *et al.* 1983, 1989), and heavy metals may be detected in them when they cannot be detected in water (Empain 1976, Say *et al.* 1981). Consequently, bryophytes are used to monitor mining and

industrial wastes (Say & Whitton 1983, Wehr & Whitton 1983a, b) and they have proved to be useful biogeochemical prospecting "tools" (Whitehead & Brooks 1969).

Most invertebrates associated with contaminated bryophytes are unlikely to be affected themselves unless they consume plant material directly, or if dissolved substances secreted by bryophytes enter other components of aquatic food webs. Gower & Darlington (1990) found that uptake of copper by larvae of the predatory caddisfly *Plectrocnemia conspersa* was primarily via the food chain, although some abiotic uptake of metal contaminants from surrounding water occurs through the insect cuticle.

As with metals, abiotic uptake is known to be responsible for the accumulation of radionuclides within bryophytes (Brown 1984, Longton 1988). For instance, following the Chernobyl accident in April 1986, fallout substantially increased levels of ^{103}Ra, ^{134}Cs and ^{137}Cs in mosses collected in Bavaria (Elstner *et al.* 1987). The accumulation of radionuclides within these plants, and within lichens, was so great that reindeer that fed on them in northern Scandinavia became heavily contaminated with ^{137}Cs. These animals are now unfit for human consumption, and fears for the continued existence of the Lapp culture which is based extensively on the use of reindeer for food, shelter and clothing have been expressed (MacKenzie 1986). Invertebrates that feed on bryophytes can also be expected to become contaminated, and spread radioactivity through aquatic food webs to fish, birds, and to species including *Homo sapiens* that prey on them.

REFERENCES

REFERENCES

Alexander C.P. (1920) *The Crane-flies of New York. Part II. Biology and Phylogeny.* Cornell University Agricultural Experimental Station, Ithaca, New York, 1129pp.

Allen E.D. & Spence D.H.N. (1981) The differential ability of aquatic plants to utilize the inorganic carbon supply in fresh waters. *New Phytologist*, **87**, 269-283

Allen H.L. (1971) Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. *Ecological Monographs*, **41**, 97-127

Allen S.E., Grimshaw H.M., Parkinson J.A. & Quarmby C. (Eds) (1974) *Chemical Analysis of Ecological Materials.*, Blackwell Scientific Publications, Oxford. 565pp.

Anderson H.W., Hoover M.D. & Reinhart K.G. (1976) *Forests and Water: Effects of Forest Management on Floods, Sedimentation and Water Supply.* U.S.D.A. Forest Service. General Technical Report PSW - 18/1976

Anderson N.H. & Sedell J.R. (1979) Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology*, **24**, 351-377

Anderson R.S. & DeHenau A.M. (1980) An assessment of the meiobenthos from nine mountain lakes in western Canada. *Hydrobiologia*, **70**, 257-264

Asakawa Y. & Heidelberger M. (1982) Chemical constituents of the Hepaticae. In: *Progress in the Chemsitry of Organic Natural Products.* (Eds W. Herz, H. Grisebach & G.W. Kirby), pp 1-269. Springer-Verlag, Wein.

Bain J.T. & Proctor M.C.F. (1980) The requirement of aquatic bryophytes for free CO_2 as an inorganic carbon source: some experimental evidence. *New Phytologist*, **86**, 393-400

Barlocher F. & Porter C.W. (1986) Digestive enzymes and feeding strategies of three stream invertebrates. *Journal of the North American Benthological Society*, **5**, 58-66

Behmer D.J. & Hawkins C.P. (1986) Effects of overhead canopy on macroinvertebrate production in a Utah stream. *Freshwater Biology*, **16**, 287-300

Benke A.C., Henry R.L. III, Gillespie D.M. & Hunter R.H. (1985) Importance of snag habitat for animal production in Southeastern streams. *Fisheries*, **10**, 8-13

Benson L.J. & Pearson R.G. (1987) The role of drift and the effect of season on macroinvertebrate colonization of implanted substrata in a tropical Australian stream. *Freshwater Biology*, **18**, 109-116

Best E.P.H. & Dassen J.H.A. (1987) Biomass, strand area, primary production characteristics and oxygen regime of the *Ceratophyllum demersum* L. in mesotrophic Lake Vechten in relation to insolation, temperature and reserve carbohydrates. *Hydrobiologia*, **148**, 231-243

Best E.P.H, Dassen J.H.A., Boon J.J. & Wiegers G. (1990) Studies on decomposition of *Ceratophyllum demersum* litter under laboratory and field conditions: losses of dry mass and nutrients, qualitative changes in organic compounds and consequences for ambient water and sediments. *Hydrobiologia*, **194**, 91-114

Bewley J.D. & Gwozdz E.A. (1975) Plant desiccation and protein synthesis. II. On the relationship between endogenous adenosine triphosphate levels and protein-synthesising capacity. *Plant Physiology*, **55**, 1110-1114

Biggs B.J.F. (1988) Artificial substrate exposure times for periphyton biomass estimates in rivers. *New Zealand Journal of Marine and Freshwater Research*, **22**, 507-515

Biggs B.J.F. (1989) Biomonitoring of organic pollution using periphyton, South Branch, Canterbury, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **23**, 263-274

Biggs B.J.F. & Close M.E. (1989) Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology*, **22**, 209-231

Bilby R.E. (1981) Role of organic debris jams in regulating the export of dissolved and particulate matter from a forested watershed. *Ecology*, **62**, 1134-1143

Bilby R.E. & Likens G.E. (1980) Importance of organic debris jams in the structure and function of stream ecosystems. *Ecology*, **60**, 1107-1113

Bird G.A. & Kaushik N.K. (1981) Coarse particulate organic matter in streams. In: *Perspectives in Running Water Ecology*. (Eds M.A. Lock & D.D. Williams), p 41-68. Plenum Press, New York.

Boling R.H., Goodman E.D., Sickle J.A., VanZimmer J.O., Cummins K.W., Petersen R.C. & Reice S.R. (1975) Toward a model of detritus processing in a woodland stream. *Ecology*, **56**, 141-151

Boothroyd I.K.G. & Dickie B.N. (1989) Macroinvertebrate colonisation of perspex artificial substrates for use in biomonitoring studies. *New Zealand Journal of Marine and Freshwater Research*, **23**, 467-478

Bott T.L., Brock J.T., Dunn C.S., Naiman R.J., Ovink R.W. & Peterson R.C. (1985) Benthic community metabolism in four temperate stream ecosystems: An interbiome comparison and evaluation of the river continuum concept. *Hydrobiologia*, **123**, 3-45

Brindle A. (1959) Notes on the larvae of the British Tipulinae (Diptera: Tipulidae). Part 7. The larvae of the *Tipula marmorata* group. *Entomologists Monthly Magazine*, **95**, 176-177

Broady P.A. (1979) Quantitative studies on the terrestrial algae of Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, **47**, 31-41

Brown D. (1984) Chapter 10. Uptake of Mineral Elements and their use in Pollution Monitoring. In: *The Experimental Ecology of Bryophytes.* (Eds A.F. Dyer & J.G. Duckett), pp.229-255. Academic Press, London.

Brusven M.A., Meeham W.R. & Biggam R.C. (1990) The role of aquatic moss on community composition and drift of fish-food organisms. *Hydrobiologia*, **196**, 39-50

Bryce D. (1957) Notes on the life histories of British Limoniinae (Diptera: Tipulidae). Part 2. *Ula sylvatica* Meigen. *Entomologists Monthly Magazine*, **93**, 132-133

Burton M.A.S. & Peterson P.J. (1979) Metal accumulation by aquatic bryophytes from polluted mine streams. *Environmental Pollution*, **19**, 39-46

Byers G.W. (1961) The Cranefly genus *Dolichopeza* in North America. *The University of Kansas Science Bulletin*, **42**, 666-807

Caldwell J.R. (1981) The Signy Island Terrestrial Reference Sites: XIII. Population dynamics of the nematode fauna. *British Antarctic Survey Bulletin*, **54**, 33-46

Carpenter K.E. (1927) Faunistic ecology of some Cardiganshire streams. *Journal of Ecology*, **15**, 33-54

Chadderton W.L. (1990) The ecology of Stewart Island freshwater communities. Unpublished MSc thesis, University of Canterbury, New Zealand. 175pp.

Chapman M.A. & Lewis M.H. (1976) *An introduction to the Freshwater Crustacea of New Zealand.* William Collins (NZ) Ltd., Auckland, 261pp.

Chinn T. (1986a) Mountain Weather. In: *The Story of Arthur's Pass National Park.* (Ed. J.Pearson), pp.24-29. Department of Lands and Survey. Cobb/Horwood Publications, Auckland. 128pp.

Chinn T. (1986b) The Shape of the Land. In: *The Story of Arthur's Pass National Park.* (Ed. J.Pearson), pp.15-23. Department of Lands and Survey and Cobb/Horwood Publications, Auckland. 128pp.

Collier K.J. (1988) Ecology of acid brownwater streams in Westland, New Zealand. Unpublished PhD thesis, University of Canterbury, New Zealand. 253pp.

Collier K.J. & Winterbourn M.J. (1987) Faunal and chemical dynamics of some acid and alkaline New Zealand streams. *Freshwater Biology*, **18**, 227-240

Conboy D.A. & Glime J.M. (1971) Effects of drift abrasives on *Fontinalis novae-angliae* Sull. *Castanea*, **36**, 111-114

Conners M.E. & Naiman R.J. (1984) Particulate allochthonous inputs: relationships with stream size in an undisturbed watershed. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 1473-1484

Cowie B. (1975) The moss fauna of a subalpine springbrook. Unpublished BSc. (Hons.) thesis, University of Canterbury, New Zealand. 30pp.

Cowie B. (1980) Community Dynamics of the Benthic Fauna in a West Coast Stream Ecosystem. Unpublished PhD. thesis, University of Canterbury, New Zealand. 200pp.

Cowie B. & Winterbourn M.J. (1979) Biota of a subalpine springbrook in the Southern Alps. *New Zealand Journal of Marine and Freshwater Research*, **13**, 295-301

Cowley D.R. (1978) Studies on the larvae of New Zealand Trichoptera. *New Zealand Journal of Zoology*, **5**, 639-750

Cox R.J. (1988) A study of the invertebrate communities associated with real and artificial bryophytes in lotic ecosystems. Unpublished PhD thesis, University of Tennessee. Memphis, Tennessee. U.S.A 163pp.

Cranston P.S. (1982) A key to the larvae of the British Orthocladiinae (Chironomidae). *Scientific Publications of the Freshwater Biological Association*, **45**, 1-163

Craw R.C. (1976) Streamside bryophyte zonations. *New Zealand Journal of Botany*, 14, 19-28

Cummins K.W. (1973) Trophic relationships of aquatic insects. *Annual Review of Entomology*, **18**, 183-206

Cummins K.W. (1974) Structure and function of stream ecosystems. *BioScience*, **24**, 631-641

Cummins K.W., Wilzbach M.A., Gates D.M., Perry J.B., & Taliaferro W.B. (1989) Shredders and riparian vegetation. *BioScience*, **20**, 365-374

Cyr H. & Downing J.A. (1988) The abundance of phtyophilous invertebrates on different species of submerged macrophytes. *Freshwater Biology*, **20**, 365-374

Dance K.W. (1981) Seasonal Aspects of Transport of Organic and Inorganic Matter in Streams. In: *Perspectives in Running Water Ecology*. (Eds M.A. Lock & D.D. Williams). pp 69-95. Plenum Press, New York.

Davis R.C. (1981) Structure and function of two Antarctic terrestrial moss communities. *Ecological Monographs*, **51**, 125-143

Dawson F.H. (1973) Notes on the production of stream bryophytes in the high Pyrenees (France). *Annales de Limnologie*, **9**, 231-240

Dean R.L. & Connell J.H. (1987a) Marine invertebrates in an algal succession. I. Variations in abundance and diversity with succession. *Journal of Experimental Marine Biology and Ecology*, **109**, 195-216

Dean R.L. & Connell J.H. (1987b) Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity with diversity. *Journal of Experimental Marine Biology and Ecology*, **109**, 249-274

Devantry P. (1987) Action des courants sur la fauna d'une mosses imergee: *Platyhypnidium riparioides* (Bryophyta). Unpublished PhD thesis, Universite Claude Bernard - Lyon 1. France. 291pp.

Dilks T.J. & Proctor M.C.F. (1975) Comparative experiments on temperature responses of bryophytes: assimilation, respiration and freezing damage. *Journal of Bryology*, **8**, 317-336

Doeg T.J., Marchant R., Douglas M. & Lake P.S. (1989) Experimental colonization of sand, gravel and stones by macroinvertebrates in the Acheron River, southeastern Australia. *Freshwater Biology*, **22**, 57-64

Douglas B. (1958) The ecology of the attached diatoms and other algae in a small stony stream. *Journal of Ecology*, **46**, 295-322

Edmonson W.T. (1944) Ecological studies of sessile Rotatoria. Part 1. Factors affecting distribution. *Ecological Monographs*, **14**,31-66

Egglishaw H.J. (1969) The distribution of benthic invertebrates on substrata in fast-flowing streams. *Journal of Animal Ecology*, **38**, 19-33

Elstner E.F., Fink R., Holl W., Lengfelder E. & Ziegler H. (1987) Natural and Chernobyl-caused radioactivity in muschrroms, mosses and soil-samples of defined biotopes in SW Bavaria. *Oecologia*, **73**, 553-558

Empain A. (1976) Les bryophytes aquatics utilises comme traceurs de la contamination en metaux lourds des eaux douces. *Memoirs de le Society Royal Botanique Belgie*, **7**, 141-156

Engel J.J. (1980) A monograph of Clasmatocolea (Hepaticae). *Fieldiana Botany*, **3**, 1-229

Erichsen-Jones J.R. (1969) A futher ecological study of the River Rheidol: the fauna of the common insects of the main stream. *Journal of Animal Ecology*, **19**, 159-177

Erman D.C. & Erman N.A. (1984) The response to stream invertebrates to substrate size and heterogeneity. *Hydrobiologia*, **108**, 75-82

Evans W.A. (1984) Seasonal abundance of the psammic rotifers of a physically controlled stream. *Hydrobiologia*, **108**, 105-114

Feeny P.P. (1976) Plant apparency and chemical defence. *Recent Advances in Phytochemistry*, **10**, 1-40

Feminella J.W., Power M.E. & Resh V.H. (1989) Periphyton responses to invertebrate grazing and riparian canopy in three northern California coastal streams. *Freshwater Biology*, **22**, 445-457

Fisher S.G. & Likens G.E. (1972) Stream ecosystem: organic energy budget. *BioScience*, **22**, 33-35

Fisher S.G. & Likens G.E. (1973) Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs*, **43**, 421-439

Fisher S.G., Gray L.J., Grimm N.B. & Busch D.E. (1982) Temporal succession in a desert stream ecosystem following flash-flooding. *Ecological Monographs*, **52**, 93-110

Fornwall M.D. (1978) Primary Productivity of *Fontinalis duriaei* Schimp. and its relation to seasonal changes in stream temperature. M.Sc thesis. Michigan Technical University.U.S.A

Fornwall M.D. & Glime J.M. (1971) Response of two species of *Fontinalis* to field isolation from stream water. *Bryologist*, **74**, 383-386

Fornwall M.D. & Glime J.M. (1982) Cold and warm-adapted phases in *Fontinalis duriaei* Schimp. as evidenced by net assimilation and respiration. *Aquatic Botany*, **13**, 165-170

Frankland J.C. (1974) Decomposition of Lower Plants. In: *The Biology of Plant Litter Decomposition*. (Eds C.H. Dickinson & C.J.F. Pugh). pp 3-36. Academic Press, London.

Frost W.E. (1939) River Liffey Survey II. The food consumed by the Brown Trout (*Salmo trutta* L.) in acid and alkaline waters. *Proceedings of the Royal Irish Academy*, **45B**, 139-206

Frost W.E. (1942) River Liffey Survey IV. The fauna of submerged "mosses" in an acid and alkaline water. *Proceedings of the Royal Irish Academy*, **47B**, 293-369

Frost W.E. (1945) Discussion on the results obtained from investigations on the food and growth of brown trout (*Salmo trutta* L.) in alkaline and acid waters. *Proceedings of the Royal Irish Academy*, **50B**, 321-342

Fuller R.L. & Stewart K.W. (1977) The food habitats of Stoneflies (Plectoptera) in the Upper Gunninson River, Colorado. *Environmental Entomology*, **6**, 293-302

Gannon J.E. (1971) Two counting cells for the enumeration of zooplankton micro-crustacea. *Transactions of the American Microscopical Society*, **90**, 486-490

Gauch H.G.J. (1986) *Multivariate Analysis in Community Ecology.* Cambridge Studies in Ecology. Cambridge University Press, Cambridge, 198pp

Geissler P. (1982) Ch 6: Alpine Communities. In: *Bryophyte Ecology.* (Ed. A.J.E. Smith). pp.179-182. Chapman and Hall, London.

Gerlach S.A. (1971) On the importance of marine meiofauna for benthos communities. *Oecologia*, **6**, 176-190

Gerlach S.A. (1978) Food chain relationships in subtidal silty and marine sediments and the role of meiofauna in stimulating bacterial productivity. *Oecologia*, **33**, 55-69

Gerson U. (1972) Chapter 9: Bryophytes and Invertebrates. In: *Bryophyte Ecology.* (Ed. A.J.E. Smith), pp.291-332. Chapman and Hall, London,New York.

Gerson U. (1985)"Mites which feed on mosses". *Proceedings of the First Bryoecological Congress*, Budapest

Gimingham C.H. & Birse E.M. (1957) Ecological studies of growth form in Bryophytes I: Correlations between growth form and habitat. *Journal of Ecology*, **45**, 533-545

Glime J.M. (1968a) Ecological observations on some bryophytes in Appalachian mountain streams. *Castanea*, **33**, 300-325

Glime J.M. (1968b) Insect communities among Appalachian Mountain stream bryophytes. Unpublished PhD thesis, Michigan State University, East Lansing, Michigan, U.S.A. 180pp.

Glime J.M. (1970) Zonation of bryophytes in the headwaters of a New Hampshire stream. *Rhodora*, **72**, 276-279

Glime J.M. (1971) Response of two species of *Fontinalis* to field isolation from stream water. *Bryologist*, **74**, 383-386

Glime J.M. (1978) Insect utilization of bryophytes. *Bryologist*, **81**, 186-187.

Glime J.M. (1984) Theories on adapations to high light intensities in the aquatic moss *Fontinalis*. *Journal of Bryology*, **13**, 257-262

Glime J.M. & Clemons R.M. (1972) Species diversity of stream insects on *Fontinalis* spp. compared to diversity on artificial substrates. *Ecology*, **53**, 458-464

Glime J.M. & Vitt D.H. (1984) The physiological adaptations of aquatic musci. *Lindbergia*, **10**, 41-52

Glime J.M., Nissila P.C., Trynoski S.E. & Fornwall M.D. (1979) A model for attachment of aquatic moss. *Journal of Bryology*, **10**, 313-320

Golterman H.L. & Clymo R.S. (Eds) (1969) *Methods for chemical analysis of fresh waters*. Blackwell Scientific Publications, Oxford, 166pp.

Gower A.M. & Darlington S.T. (1990) Relationships between copper concentrations in larvae of *Plectrocnemia conspersa* (Curtis) (Trichoptera) and in mine drainage streams. *Environmental Pollution*, **65**, 155-168

Graesser A.K. (1988) Physico-chemical conditions and benthic community dynamics in four South Westland streams. Unpublished PhD thesis, University of Canterbury, New Zealand. 203pp.

Gregg W.W. & Rose F.L. (1985) Influences of aquatic macrophytes on invertebrate community structure, guild structure, and microdistribution in streams. *Hydrobiologia*, **128**, 45-56

Griffiths B.S. & Cheshire M.V. (1987) Digestion and excretion of nitrogen and carbohydrate by the cranefly larva *Tipula paludosa* (Diptera: Tipulidae). *Insect Biochemistry*, **17**, 277-282

Harding M.A. (1990) Observations of fruit eating by Blue Duck. *Notornis*, **37**, 150-152

Harrod J.J. (1964) The distribution of invertebrates on submerged aquatic plants in a chalk stream. *Journal of Animal Ecology*, **33**, 335-348

Hart D.D. (1978) Diversity in stream insects: regulation by rock size and microspatial complexity. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **20**, 1376-1381

Hasler A.D. (1938) Fish biology and limnology of Crater Lake, Oregon. *Journal of Wildlife Management*, **2**, 94-103

Heede B.H. (1972) Influence of a forest on the hydraulic geometry of two mountain streams. *Water Resources Bulletin*, **8**, 523-530

Heywood J. (1362) "The rolling stone never gathereth moss" In Stevenson B. (1947) *The Home Book of Quotations, Classical and Modern.* Dodd, Mead and Company, New York, 2812 pp.

Higgins R.D. (1959) Life history of *Macrobiotis islandicus* Richters, with notes on other Tardigrades from Colorado. *Transactions of the American Microscopical Society* **78**, 137-154

Hill M.O. (1979a) DECORANA - A FORTRAN Program for Detrended Correspondence Analysis and Reciprocal Averaging. Cornell University, Ithaca, New York.

Hill M.O. (1979b) TWINSPAN - A FORTRAN Program for Averaging Multivariate Data in an Ordered Two-way Table by classification of the Individuals and Attributes. Cornell University, Ithaca, New York.

Hill W.R. & Knight A.W. (1987) Experimental analysis of the grazing interaction between a mayfly and stream algae. *Ecology*, **68**, 1955-1965

Hogue E.W. & Miller C.B. (1981) Effects of sediment microtopography on small-scale spatial distributions of meiobenthic nematodes. *Journal of Experimental Marine Biology and Ecology*, **53**, 181-191

Horning D.J., Schuster R.O. & Grigarick A.A. (1978) Tardigrada of New Zealand. *New Zealand Journal of Zoology*, **5**, 185-280

Hutchinson G.E. (1975) *A Treatise on Limnology. Vol. III. Limnological Botany.* John Wiley and Sons, Inc., New York, 660pp.

Hynes H.B.N. (1961) The invertebrate fauna of a Welsh mountain stream. *Archiv für Hydrobiologie*, **57**, 344-388

Hynes H.B.N. (1975) The stream and its valley. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **19**, 1-15

Inoue H. & Schuster R.M. (1971) A momograph of the New Zealand and Tasmanian Plaglochilaceae. *Journal of the Hattori Botanical Laboratory*, **34**, 1-225

Jacoby J.M. (1985) Grazing effects on periphyton by *Theodoxus fluvitalis* (Gastropoda) in a lowland stream. *Journal of Freshwater Ecology*, **3**, 265-274

Jacoby J.M. (1987) Alterations in periphyton characteristics due to grazing in a Cascade foothill stream. *Freshwater Biology*, **18**, 495-508

Jennings P.G. (1976) Tardigrada from the Antarctic Peninsula and Scotia Ridge region. *British Antarctic Survey Bulletin*, **44**, 77-95

Jennings P.G. (1979) The Signy Island terrestrial reference sites: X. Population dynamics of Tardigrada and Rotifera. *British Antarctic Survey Bulletin*, **47**, 89-105

Johnson T. (1978) Aquatic mosses and stream metabolism in a North Swedish river. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **20**, 1471-1477

Jones D.H. (1986) The effect of afforestation on fresh waters in Tayside, Scotland. Zooplankton and other microfauna. *Hydrobiologia*, **133**, 223-235

Kear J. & Burton P.J.K. (1971) The food and feeding apparatus of the Blue Duck *Hymenolaimus*. *Ibis*, **113**, 483-493

Keller E.A. & Swanson F.J. (1979) Effects of large organic material on channel form and fluvial processes. *Earth Surface Processes*, **4**, 361-380

Keller E.A. & Tally T. (1979) Effects of large organic debris on channel form and fluvial processes in the coastal redwood environment. In: *Adjustments on the Fluvial System*. (Eds D.D. Rhodes & G.P. Williams). p 66-70. State University of New York, Binghamton,New York.

Kelly M.G. & Whitton B.A. (1987) Growth rate of the aquatic moss *Rhynchosteigium riparioides* in Northern England. *Freshwater Biology*, **18**, 461-468

King D.K. & Cummins K.W. (1989) Autotrophic-Heterotrophic community metabolism relationships of a woodland stream. *Journal of Freshwater Ecology*, **5**, 205-218

Korotokevich V.S. (1964) Concerning the population of water bodies in the oases of East Antarctica. *Soviet Antarctic Expedition Information Bulletin*, **1**, 154-161

Krecker F.H. (1939) A comparative study of the animal population of certain submerged aquatic plants. *Ecology*, **20**, 553-562

Krocho J.E., Bewley J.D. & Pacey J. (1978) The effects of rapid and very slow speeds of drying on the ultrastructure and metabolism of the desiccation sensitive moss *Cratoneuron filiculum* (Hedw) Spruce. *Journal of Experimental Botany*, **29**, 905-917

Krupa J. (1977) The interdependence between transpiration intensity and the anatomical structure of moss leaves. *Acta Societatis Botanicorum Poloniae*, **46**, 57-68

Lamberti G.A. & Resh V.H. (1985) Comparability of introduced tiles and natural substrates for sampling lotic bacteria, algae and macroinvertebrates. *Freshwater Biology*, **15**, 21-30

Lawrey J.D. (1987) Nutritional Ecology of Lichen/Moss Arthropods. In: *Nutritional Ecology of Insects, Mites, Spiders, and related invertebrates.* (Eds F. Slansky Jr. & J.G. Rodriguez). p 209-233. John Wiley & Sons, New York.

Light J.J. (1975) Clear lakes and aquatic bryophytes in the mountains of Scotland. *Journal of Ecology*, **63**, 937-943

Light J.J. & Lewis-Smith R.I. (1976) Deep-water bryophytes from the highest Scottish lochs. *Journal of Bryology*, **9**, 55-62

Lillehammer A. (1966) Bottom fauna investigations in a Norwegian river. *Nytt Magasin for Zoologi*, **12**, 10-29

Lindegaard C., Thorup & Bahn M. (1975) The invertebrate fauna of the moss carpet in the Danish spring Ravnkilde and its seasonal, vertical and horizontal distribution. *Archiv für Hydrobiologie*, **75**, 109-139

Longton R.E. (1988) *The Biology of Polar Bryophytes and Lichens.* Cambridge University Press, Cambridge, 391pp.

Lyford J.H. & Gregory S.V. (1975) The dynamics and structure of periphyton communities in three Cascade Mountain streams. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **19**, 1610-1616

Maberly S.C. (1985a) Photosynthesis by *Fontinalis antipyretica*: I. Interaction between photon irradiance, concentration of carbon dioxide and temperature. *New Phytologist*, **100**, 127-140

Maberly S.C. (1985b) Photosynthesis by *Fontinalis antipyretica*: II. Assessment of environmental factors limiting photosynthesis and production. *New Phytologist*, **100**, 141-155

MacKenzie D. (1986) The rad-dosed reindeer. *New Scientist*, **1539**, 37-40

Marchant R. (1990) Robustness of classification and ordination techniques applied to macroinvertebrate communities from the La Trobe River, Victoria. *Australian Journal of Marine and Freshwater Research*, **41**, 493-504

Markham K.R. & Porter L.J. (1978) Chemical constituents of the bryophytes. *Progress in Phytochemistry*, **5**, 181-273

Martin C.E. (1980) Chlorophyll *a/b* ratios of eleven North Carolina mosses. *Bryologist*, **83**, 84-87

Martin C.E. & Churchill S.P. (1982) Chlorophyll concentrations and *a/b* ratios in mosses collected from exposed and shaded habitats in Kansas. *Journal of Bryology*, **12**, 297-304

Martin W.M. (1946) The moss flora of the Arthurs Pass National Park. *Transactions of the Royal Society of New Zealand*, **76**, 37-57

Maslen N.R. (1981) The Signy Island Terrestrial Reference Sites: XII. Population ecology of nematodes with additions to the fauna. *British Antarctic Survey Bulletin*, **53**, 57-75

Maurer M.A. & Brusven M.A. (1983) Insect abundance and colonization rate in *Fontinalis neo-mexicana* (Bryophyta) in an Idaho Batholith stream, U.S.A. *Hydrobiologia*, **98**, 9-15

McAuliffe (1983) Competition, colonization patterns, and disturbance in stream benthic communities. In: *Stream Ecology. Application and Testing of General Ecological Theory*. (Eds J.R. Barnes & G.W. Minshall), pp 137-156. Plenum Press., New York.

McCammon R.G. (1978) Organic energy flow in a mountian beech forest stream ecosystem. Unpublished MSc. thesis, University of Canterbury, Christchurch, New Zealand. 158pp.

McCune B. (1987) Multivariate Analysis on the PC-ORD system. A software documentation report. Unpublished Holcomb Research Institute Report No 75., Butler University, Indiana. U.S.A. 122pp.

McElhone M.J. & Davies R.W. (1983) The influence of rock surface area on the microdistribution and sampling of attached riffle dwelling Trichoptera in Hartley Creek, Alberta. *Canadian Journal of Zoology*, **61**, 2300-2304

McFarlane A.G. (1951) Caddisfly larvae (Trichoptera) of the Family Rhyacophilidae. *Records of the Canterbury Museum*, **5**, 267-289

McIntire C.D. (1973) Periphyton dynamics in laboratory streams: a simulation model and its implications. *Ecological Monographs*, **43**, 399-420

McKenzie-Smith F. (1987) Aquatic bryophytes as habitat for invertebrates in a Victorian upland stream. Unpublished BSc.(Hons.) thesis, Monash University, Melbourne, Australia. 104pp.

Meier P.G., Penrose D.L. & Polak L. (1979) The rate of colonization by macro-invertebrates on artificial substrate samplers. *Freshwater Biology*, **9**, 381-392

Meyer M.S. & Likens G.E. (1987) The importance of algae in a shaded headwater stream as food for an abundant caddisfly (Trichoptera). *Journal of North American Benthological Society*, **6**, 262-269

Metzler G.M. & Smock L.A. (1990) Storage and dynamics of subsurface detritus in a sand-bottomed stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 588-594

Minshall G.W. (1984) Aquatic Insect-Substratum Relationships. In: *The Ecology of Aquatic Insects*. (Eds V.H. Resh & D.M. Rosenberg). pp 358-400. Praeger, New York.

Molles M.C. Jr. (1982) Trichopteran communities of streams associated with Aspen and Conifer forests: long-term structural change. *Ecology*, **63**, 1-6

Morgan C.I. & King P.E. (1976) British Tardigrades. In: *Synopsis of the British Fauna (New Series)*. (Ed. D.M. Kermack). Academic Press Inc., London. 133pp.

Murphy M.L. & Hall J.D. (1981) Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 137-145

Mutch R.A. & Pritchard G. (1984a) The life history of *Philocasca alba* (Trichoptera: Limnephilidae) in a Rocky Mountain stream. *Canadian Journal of Zoology*, **62**, 1282-1288

Mutch R.A. & Pritchard G. (1984b) The life history of *Zapada columbriana* (Plecoptera:Nemouridae) in a Rocky Mountain stream. *Canadian Journal of Zoology*, **62**, 1273-1281

Naiman R.J. (1983) The annual pattern and spatial distribution of aquatic metabolism in boreal forest watersheds. *Ecological Monographs*, **53**, 73-94

O'Brien T.P. & McCully M.E. (1981) *The Study of Plant Structure. Principles and Selected Methods.* Termarcarphi Pty Ltd, Melbourne, Australia. 342pp.

O'Doherty E.C. (1985) Stream-dwelling copepods - their life history and ecological significance. *Limnology and Oceanography*, **30**, 554-565

Odu E.A. (1978) The adaptive importance of moss rhizoids for attachment to the substratum. *Journal of Bryology*, **10**, 163-181

Ogilvie G.A. & Clifford H.F. (1986) Life histories, production, and microdistribution of two caddisflies (Trichoptera) in a Rocky Mountain stream. *Canadian Journal of Zoology*, **64**, 2706-2716

O'Hop J., Wallace J.B. & Haeffner J.D. (1984) Production of a stream shredder, *Pettoperla maria* (Plecoptera: Pettoperlidae) in disturbed and undisturbed hardwood catchments. *Freshwater Biology*, **14**, 13-21

Ordish R.G. (1984) Hydraenidae (Insecta: Coleoptera). *Fauna of New Zealand*, **6**, 56pp

Ormerod S.J., Wade K.R. & Gee A.S. (1987) Macro-floral assemblages in upland Welsh streams in relation to acidity, and their importance to invertebrates. *Freshwater Biology*, **18**, 545-557

Pant B.G. & Tewin S.D. (1984) On some aquatic bryophyte communities of Nainital and its environs (Western Himalayas). *Geophytology*, 14, 137-142

Percival E. & Whitehead H. (1929) A quantitative study of the fauna of some types of stream-bed. *Journal of Ecology*, **17**, 282-314

Percival E. & Whitehead H. (1930) Biological survey of the River Wharfe. II. Report on the invertebrate fauna. *Journal of Ecology*, **18**, 288-314

Pfankuch D.J. (1975) Stream reach inventory and channel stability evaluation. U.S.D.A. Forest Service, Region 1, Missoula, Montana, U.S.A. 26pp

Pritchard G. (1983) Biology of Tipulidae. *Annual Review of Entomology*, **28**, 1-22

Pomogyi P., Best E.P.H., Boon J.J. & Dassen J.H.A. (1984) On the relation between age, plant composition and nutrient release from living and killed *Ceratophyllum* plants. *Aquatic Botany*, **12**, 243-250

Reiter M.A. & Carlson R.E. (1986) Current velocity in streams and the composition of benthic algal mats. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 1156-1162

Rhoades D.F. & Cates R.G. (1976) Toward a general theory of plant antiherbivore chemistry. *Recent Advances in Phytochemistry*, **10**, 168-213

Roby K.B., Newbold J.D. & Erman D.C. (1978) Effectiveness of an artificial substrate for sampling macroinvertebrates in small streams. *Freshwater Biology*, **8**, 1-8

Rogers K.H. & Breen C.M. (1983) Chapter 27. An investigation of macrophyte, epiphyte and grazer interactions. In: *Periphyton of freshwater ecosystems. Developments in Hydrobiology 17* (Wetzel), p.217-226. Dr W.Junk Publishers, The Hague.

Rooke J.B. (1984) The invertebrate fauna of four macrophytes in a lotic system. *Freshwater Biology*, **14**, 507-513

Rooke J.B. (1986a) Seasonal aspects of the invertebrate fauna of three species of plants and rock surfaces in a small stream. *Hydrobiologia*, **134**, 81-87

Rooke J.B. (1986b) Macroinvertebrates associated with macrophytes and plastic immitations in the Eramosa River, Ontario, Canada. *Archiv für Hydrobiologie*, **106**, 307-325

Rosenthal G.A. & Janzen D.H. (1979) *Herbivores: Their Interaction with Secondary Plant Metabolites*. Academic Press, New York, 738pp.

Rosine W.N. (1955) The distribution of invertebrates on submerged aquatic surfaces in Muskee Lake, Colorado. *Ecology*, **36**, 308-314

Rounick J.S. (1982) An investigation of carbon pathways in New Zealand streams. Unpublished PhD. thesis, University of Canterbury, New Zealand. 153pp.

Rounick J.S. & Winterbourn M.J. (1982) Benthic faunas of forested streams and suggestions for their management. *New Zealand Journal of Ecology*, **5**, 140-150

Rounick J.S. & Winterbourn M.J. (1983) The formation, structure and utilization of stone surface organic layers in two New Zealand streams. *Freshwater Biology*, **13**, 57-72

Rounick J.S. & Winterbourn M.J. (1986) Stable carbon isotopes and carbon flow in ecosystems. *BioScience*, **36**, 171-177

Rounick J.S., Winterbourn M.J. & Lyon G.L. (1982) Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. *Oikos*, **39**, 191-198

Rundle S.D. & Hildrew A.G. (1990) The distribution of micro-arthropods in some southern English streams: the influence of physiochemistry. *Freshwater Biology*, **23**, 411-431

Russo A.R. (1990) The role of seaweed complexity in structuring Hawaiian epiphytal amphipod communities. *Hydrobiologia*, **194**, 1-12

Sartory D.P. & Grobbelaar J.U. (1984) Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiologia*, **114**, 177-187

Sarvala J. (1979) Effect of temperature on the duration of egg, nauplius and copepodite development of some freshwater benthic Copepoda. *Freshwater Biology*, **9**, 515-534

Sarvala J. (1986) Patterns of benthic copepod assemblages in an oligotrophic lake. *Annales Zoologici Fennici*, **23**, 101-130

SAS Institute Inc. (1988) SAS/STAT Users Guide, Release 6.03 Edition. Sas Institute: Cary, North Carolina. U.S.A. 1028pp

Satake K., Soma M., Seyama H. & Uehiro T. (1983) Accumulation of mercury in the liverwort *Jungermannia vulcanicola* Say. in an acid stream Kashiranashigawa in Japan. *Archive für Hydrobiologia*, **99**, 80-92

Satoke K., Takamatsu T., Soma M., Shibata K., Nishikawa M., Say P.J. & Whitton B.A. (1989) Lead accumulation and location in the shoots of the aquatic liverwort *Scapania undulata* (L.)Dum. in stream water at Greenside Mire, England. *Aquatic Botany*, **33**, 111-122

Say P.J. & Whitton B.A. (1983) Accumulation of heavy metals by aquatic mosses. 1: *Fontinalis antipyretica* Hedw. *Hydrobiologia*, **100**, 245-260

Say P.J., Harding J.P.C. & Whitton B.A. (1981) Aquatic mosses as monitors of heavy metal contamination in the River Etherow, England. *Environmental Pollution Series B*, **2**, 295-307

Schofield W.B. (1985) Chapter 22. Chemistry. In: *Introduction to bryology*. p.273-282. McMillian Publishing Company, New York.

Scott G.A.M., Stone I.G. & Rosser C. (1976) *The Mosses of Southern Australia*. Academic Press, London, 495pp.

Scott G.A.M. (1985) *Southern Australian Liverworts*. Australian Government Printing Service, Canberra, 216pp.

Scrimgeour G.J. & Winterbourn M.J. (1989) Effects of floods on epilithon and benthic macroinvertebrate populations in an unstable New Zealand river. *Hydrobiologia*, **171**, 33-44

Scrimgeour G.J., Davidson R.J. & Davidson J.M. (1988) Recovery of benthic macroinvertebrate and epilithic communities following a large flood, in an unstable, braided, New Zealand river. *New Zealand Journal of Marine and Freshwater Research*, **22**, 337-344

Sedell J.R., Triska F.J., Hall J.D., Anderson N.H. & Lyford J.H. (1974) Sources and fates of organic inputs in coniferous forest streams. In: *Integrated Research in the Coniferous Forest Biome*. (Eds R.H. Waring & R.L. Edmonds). p.57-69. US/IBP Bulletin No 5, Seattle.

Sedell J., Bisson P., Swanson F.J. & Gregory S.V. (1988) What we know about large trees that fall into streams and rivers. In: *From the forest to the sea: a story of fallen trees*. (Eds C. Maser, R.F. Torrant, J.M. Trappe & J.F. Franklin) pp 47-79. USDA Forest Service General Technical Report PNW-GTR-229, Pacific Northwest Research Station, Portland, Oregon.

Sheath R.G., Burkholder J.M., Hambrook J.A., Hogeland A.M., Hoy E., Kane M.E., Morison M.O., Steinman A.D. & Van Alstyne K.L. (1986) Characteristics of softwater streams in Rhode Island. III. Distribution of macrophytic vegetation in a small drainage basin. *Hydrobiologia*, **140**, 183-191

Sheldon A.L. (1984) Colonization dynamics of aquatic insects. In: *The Ecology of Aquatic Insects.* (Eds V.H. Resh & D.M. Rosenberg). pp 401-429. Praeger., New York.

Shiozawa D.K. (1986) The seasonal community structure and drift of microcrustaceans in Valley Creek, Minnesota. *Canadian Journal of Zoology*, **64**, 1655-1664

Sinsabaugh R.L., Linkins E. & Benfield E.F. (1985) Cellulose digestion and assimilation by three leaf-shredding aquatic insects. *Ecology*, **66**, 1464-1471

Slack N.G. & Glime J.M. (1985) Niche relationships of mountain stream bryophytes. *Bryologist*, **88**, 7-18

Smith B.P. (1988) Host-parasite interaction and impact of larval water mites on insects. *Annual Review of Entomology* **33**, 482-507

Smith D.G., Macaskill J.B., Stevenson C.D. & Edgerley W.H.L. (1982) *Physical and Chemical Methods for Water Quality Analysis.* Water and Soil Division, Ministry of Works and Development, Wellington, 158pp.

Smith-Cuffney F.L. (1987) Ecological interactions in the moss habitat of streams draining a clearcut and a reference watershed. Unpublished PhD thesis, University of Georgia. Athens, Georgia. U.S.A. 174pp.

Sohlenius B. (1979) A carbon budget for nematodes, rotifers and tardigrades in a Swedish coniferous forest soil. *Holarctic Ecology*, **2**, 30-40

Sohlenius B. (1980) Abundance, biomass and contribution to energy flow by soil nematodes in terrestrial ecosystems. *Oikos*, **34**, 186-194

Sokal R.R. & Rohlf F.J. (1981) *Biometry. The Principles and Practice of Statistics in Biological Research.* W.H.Freeman and Company, San Francisco, 859pp.

Spaul V.W. (1973) Distribution of nematode feeding groups at Signy Island, South Orkney Islands, with an estimate of their biomass and oxygen consumption. *British Antarctic Survey Bulletin*, **37**, 21-32

Speaker R., Moore K. & Gregory S. (1984) Analysis of process of retention of organic matter in steam ecosystems. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **22**, 1835-1841

Speaker R.W., Luchessa K.J., Franklin J.F. & Gregory S.V. (1988) The use of plastic strips to measure leaf retention by riparian vegetation in a coastal Oregon stream. *American Midland Naturalist*, **120**, 22-31

Stern M.S. & Stern D.H. (1969) A Limnological study of a Tennessee cold springbrook. *American Midland Naturalist*, **82**, 62-82

Strayer D. & Likens G.E. (1986) An energy budget for the zoobenthos of Mirror Lake, New Hampshire. *Ecology*, **67**, 303-313

Suire C., Barriere G., Comps B. & Letouzey-Dulau J. (1975) Ecological research on the bryophytes of forest groups in South-Western France. *Review of Bryology and Lichenology*, **41**, 283-302

Suren A.M. (1990) Microfauna associated with algal mats in melt ponds of the Ross Ice Shelf. *Polar Biology*, **10**, 329-335

Terra W.R. (1990) Evolution of digestive systems of insects. *Annual Review of Entomology*, **35**, 181-200

Tett P., Gallegus C., Kelly M., Homberger M. & Cosby B.G. (1978) Relationships among substrate flow and benthic microalgal pigment density in the Mechums River, Virginia. *Limnology and Oceanography*, **23**, 785-797

Thienemann A. (1912) Der Bergbach des Sauerlandes. Faunistisch biologische Untersuchungen. *Internatinalen Revue fur Biologische, Supplementband*, **4**, 1-125

Thomas J.D. (1987) An evaluation of the interactions between freshwater pulmonate snail hosts of human schistosomes and macrophytes. *Philosophical Transactions of the Royal Society of London. Series B*, **315**, 75-125

Thorup J. & Lindegaard C. (1977) Studies on Danish springs. *Folia Limnologica Scandinavica*, **17**, 7-15

Tokeshi M. & Pinder L.C.V. (1985) Microhabitats of stream invertebrates on two submerged macrophytes with contrasting leaf morphology. *Holarctic Ecology*, **8**, 313-319

Towns D.R. (1979) Composition and zonation of benthic invertebrate communities in a New Zealand kauri forest stream. *Freshwater Biology*, **9**, 251-262

Townsend C.R. (1989) The patch dynamics concept of stream community ecology. *Journal of North American Benthological Society*, **8**, 36-50

Traaen T.S. & Lindstrom E.-A. (1983) Chapter 13: Influence of current velocity on periphyton distribution. In: *Periphyton of Freshwater Ecosystems. Developments in Hydrobiology 17.* (Ed R.G. Wetzel). pp 97-99. Dr W.Junk Publishers, The Hague.

Trotter E.H. (1990) Woody debris, forest-stream succession, and catchment geomorphology. *Journal of North American Benthological Society*, **9**, 141-156

Tutin W. (1949) The moss ecology of a lakeland stream. *Transactions of the British Bryological Society*, **1**, 166-171

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 130-137

Vitt D.H. & Glime J.M. (1984) The structural adaptations of aquatic musci. *Lindbergia*, **10**, 95-110

Wehr J.D. & Whitton B.A. (1983a) Accumulation of heavy metals by aquatic mosses. 2: *Rhynchosteglum riparioides*. *Hydrobiologia*, **100**, 261-284

Wehr J.D. & Whitton B.A. (1983b) Accumulation of heavy metals by aquatic mosses. 3: Seasonal changes. *Hydrobiologia* **100**, 285-291

Weiser W. (1952) Investigations on the microflora inhabitating seaweeds on rocky coasts. *Journal of the Marine Biology Association*, **31**, 145-174

Welch H.E. (1976) Ecology of Chironomidae (Diptera) in a Polar Lake. *Journal of the Fisheries Research Board of Canada.*, **33**, 227-247

Wetzel R.G. (1969) Factors influencing photosynthesis and excretion of dissolved organic matter by aquatic macrophytes in hard-water lakes. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **17**, 72-85

Wetzel R.G. (1983) Chapter 26. Attached algae-substrata interactions: fact or myth, and when and how? In: *Periphyton of Freshwater Ecosystems. Developments in Hydrobiology.* (Ed. R.G. Wetzel). pp 207-215. Dr W.Junk Publishers., The Hague.

Whitehead N.E. & Brooks R.R. (1969) Aquatic bryophytes as indicators of uranium mineralization. *Bryologist*, **72**, 501-507

Whitton B.A., Say P.J. & Jupp J.D. (1982) Accumulation of zinc, cadmium and lead by the aquatic liverwort *Scapania*. *Environmental Pollution Series B*, **3**, 299-316

Williams D.D. & Williams N.E. (1982) Morphological and dietary variations in a riverine population of *Pycnopsyche guttifer* (Trichoptera: Limnephilidae). *Aquatic Insects*, **4**, 21-27

Williams D.H. (1989) Towards a biological and chemical definition of the hyporheic zone in two Canadian rivers. *Freshwater Biology*, **22**, 189-208

Williams D.H. & Hynes H.B.N. (1974) The occurrence of benthos in the substratum of a stream. *Freshwater Biology*, **4**, 233-256

Williams M. (1985) Blue Duck- a declining species? In: Wildlife in New Zealand. New Zealand Wildlife Service. Department of Internal Affairs Report. 4pp.

Willoughby L.G. & Mappin R.G. (1988) The distribution of *Ephemerella ignita* (Ephemeroptera) in streams: the role of pH and fod resources. *Freshwater Biology*, **19**, 145-155

Winner J.M. (1975) Chapter 7. Zooplankton. In: *River Ecology. Studies in Ecology.* (B.A. Whitton), pp. 155-170. University of California Press., Berkeley and Los Angeles.

Winterbourn M.J. (1976) Fluxes of litter falling into a small beech forest stream. *New Zealand Journal of Marine and Freshwater Research*, **10**, 399-416

Winterbourn M.J. (1978) An evaluation of the mesh bag method for studying leaf colonization by stream invertebrates. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **20**, 1557-1561

Winterbourn M.J. (1982a) Food utilization by a stream detritivore, *Zelandopsyche ingens* (Trichoptera: Oeconesidae). *Internationale Revue gestmaten Hydrobiologie*, **67**, 209-222

Winterbourn M.J. (1982b) The invertebrate fauna of a forest stream and its association with fine particulate organic matter. *New Zealand Journal of Marine and Freshwater Research*, **16**, 271-281

Winterbourn M.J. (1986) Chapter XI. Recent advances in our understanding of stream ecosystems. In: *Ecosystem Theory and Application*. (Ed. N. Polunin). pp240-268. John Wiley and Sons Ltd., New York.

Winterbourn M.J. (1990) Interactions among nutrient, algae and invertebrates in a New Zealand mountain stream. *Freshwater Biology*, **23**, 463-474

Winterbourn M.J. & Davies S.F. (1976) Ecological role of *Zelandopsyche ingens* (Trichoptera: Oeconesidae) in a beech forest stream ecosystem. *Australian Journal of Marine and Freshwater Research*, **27**, 197-215

Winterbourn M.J. & Gregson K.L.D. (1989) Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand*, **9**, 1-96

Winterbourn M.J. & Rounick J.S. (1985) Benthic faunas and food reserves of insects in small New Zealand streams subjected to different forestry practices. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **22**, 2148-2152

Winterbourn M.J., Rounick J.S. & Cowie B. (1981) Are New Zealand stream ecosystems really different? *New Zealand Journal of Marine and Freshwater Research*, **15**, 321-328

Winterbourn M.J., Rounick J.S. & Hildrew A.G. (1986) Patterns of carbon utilization by benthic invertebrates in two British river systems: a stable carbon isotope study. *Archive für Hydrobiologie*, **107**, 349-361

Winterbourn M.J., Collier K.J. & Graesser A.K. (1988) Ecology of small streams on the west coast of the South Island, New Zealand. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **23**, 1427-1431

Wyatt R. & Stoneburner A. (1989) Bryophtyophagy of *Rhizomnium punctatum* by larvae of the cranefly *Tipula oropezoides*. *Bryologist*, **92**, 308-309

Young S.A., Kovalak W.D. & DelSignore K.A. (1978) Distances travelled by autumn-shed leaves introduced into a woodland stream. *American Midland Naturalist*, **100**, 217-222

Zar J.H. (1984) *Biostatistical Analysis*. Prentice-Hall International, Inc, London, 718pp.

Zullini A. (1976) Nematodes as indicators of river pollution. *Nematologica Mediterranea*, **4**, 13-22

Zullini A. & Ricci C. (1980) Bdelloid rotifers and nematodes in a small Italian stream. *Freshwater Biology*, **10**, 67-72

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APPENDIX ONE:

LIST OF TAXA ENCOUNTERED

DURING THE STUDY

Systematic list of invertebrate taxa collected from bryophyte and riffle habitats in the two study streams in Arthurs Pass National Park from July 1986 to December 1987.

*denotes lowest taxonomic level used in the analysis of the 18 month survey data.

**indicates that although identification of larger instar larvae of these genera was possible, most individuals were too small for accurate identification. Thus all species were treated as 1 taxon in all quantitative analyses.

***Mites were grouped into a single OTU for the analysis of the 18 month survey data. However, in the meiofaunal investigation (Chapter 3), mite taxa were treated separately.

Phylym NEMATODA
Class **Dorylaimoidea**
* Order DORYLAIMIDA
Phylum NEMATOMORPHA
* Class **Gordiidae**

Phylum ROTIFERA
Class **Digononta**
* Order BDELLOIDEA
Phylum TARDIGRADA
Order EUTARDIGRADA
Fam Macrobiotoidae
Macrobiotis dispar (Murray)

Phylum PLATYHELMINTMES
Class **Turbellaria**
Order TRICLADIDA
Neppia montana (Nurse)

Phylum ANNELIDA
* Class **Oligochaeta**

Phylum ARTHROPODA
Class **Insecta**
Order COLLEMBOLA
SpA Poduridae
SpB Isotomidae
SpC Sminthuridae

Order EPHEMEROPTERA
Fam Leptophlebiidae
Deleatidium spp.

Fam Siphlonuridae
Nesameletus spp.

Order PLECOPTERA
Fam Eustheniidae
Stenoperla prasina (Newman)

Fam Austroperlidae
Austroperla cyrene (Newman)

Fam Gripopterygidae
Megaleptoperla grandis (Kimmins)
** ⌈ *Zelandoperla fenestrata* Tillyard
⌊ *Z. decorata* Tillyard

⌈ *Zelandobius confusus* (Hare)
** *Z. furcillatus* Tillyard
⌊ *Z. unicolor* Tillyard

Acroperla spiniger (Tillyard)
A. trivacuata (Tillyard)

Fam Notonemouridae
Spaniocercoides ?hudsoni (Kimmins)
Cristaperla fimbria (Winterbourn)
Halticoperla viridans (McLellan & Winterbourn)
Spaniocerca zelandica (Tillyard)

Order TRICHOPTERA
Fam Hydrobiosidae
Tiphobiosis sp.
Psilochorema sp.
Costachorema brachyptera McFarlane
C. xanthoptera McFarlane
C. callista McFarlane
Hydrobiosis silvicola McFarlane
H. clavigera McFarlane
H. parumbripennis McFarlane
H. charadraeae McFarlane
H. spatulata McFarlane
H. harpidosa McFarlane
Edpercivalia maxima McFarlane
Hydrochorema crassicaudatum Tillyard
** Small unidentified larvae
Unidentified pupae

Fam Hydropsychidae
Aoteapsyche colonica (McLachlan)

Fam Oeconesidae
Zelandopsyche ingens Tillyard
Oeconesus? similis Mosley

Fam Philorheithridae
Philorheithris agilis (Hudson)

Fam Helicophidae

** [*Zelolessica cheira* McFarlane
| *Zelolessica* sp.

Fam Conoesucidae

Pycnocentrodes sp.
Pycnocentria funerea McLachlan

** [*P. sylvestris* McLachlan
| *P. evecta* McLachlan

Olinga feredayi (McLachlan)

Order COLEOPTERA

Fam Hydraenidae

Orchymontia calcarata
Homalaena dispersa

Fam Elmidae - adults
- larvae

Fam Scirtidae sp.A[1]
(= Helodidae) sp.B[1]
sp.C[1]

Hydrophilidae Larvae
Ptilodactylidae larvae

Order NEUROPTERA

Kempynus sp.

Order DIPTERA

Fam Tipulidae

Limonia hudsoni - larvae (Edwards)
- pupae

Aphrophilia neozelandica (Edwards)
Hexatomini
Paralimnophila skusei Hutton
Eriopterini

Fam Blephariceridae

Neocurupira campbelli Dumbleton

Fam Dixidae

Nothodixa campbelli (Alexander)

Fam Simuliidae

Austrosimulium ungulatum Tonnoir

* Fam: Chironomidae - larvae *Heptagyini* spp.
Eukiefferiella claripennis
Maoridiamesia sp.
Rheocricotopus sp.
- pupae
- adults

Fam Ceratopogonidae
Fam Empididae spA - G
- pupae

Fam Muscidae spA - D

Fam Psychodidae

Fam Stratiomyidae

Class **Crustacea**
* Subclass Ostracoda
* Subclass Copepoda
Order EUCOPEPODA
Suborder Harpacticoidea
Fam Canthocamptidae
Canthocamptus? howardorum
C. ?maoricus
Antarctobiotus elongatus Lewis
Antarctobiotus sp. (cf *diversus* Lewis)
Attheyella stillicidarum Lewis
Attheyella sp. (cf *brehmi* Chappuis)

Subclass Isopoda
Styloniscus otakensis (Chilton)

*** Class **Arachniida**
Order ACTINEDIDA
Fam Anisitsiellidae
Anisitsiellides sp. A
Anisitsiellides sp. B

Fam Aturidae
Paratryssaturus sp.
Pseudotryssaturus acutus Cook

Fam Hydraphantidae
Euwandesia sp.
Indet.gen. et sp.
Notopanisus sp.

Fam Hygrobatidae
Zelandobatella naias Hopkins

Fam Mideopsidae
Guineaxonopsis serratiplpis Cook

Fam Momoniidae
Neomomonia sp.

Super Fam Trombidioidea
- several species indet.

Order Oribatida
- several species indet.

[1] As in Winterbourn & Gregson 1990

APPENDIX TWO:

STABILITY OF CHLOROPHYLL IN ETHANOL

EXTRACTIONS OF BENTHIC ALGAE

INTRODUCTION

Chlorophyll *a* is frequently used as an index of algal biomass (Vollenweider 1969). However, its concentration in algal cells is somewhat variable, and depends on the species involved and their physiological states. Ninety percent acetone has been the principal solvent for extraction of chlorophyll, initially without correction for the presence of phaeopigments (Richards & Thompson 1952, Strickland & Parsons 1968). However, pre and post acidification methods (Lorenzen 1967, Wetzel & Westlake 1969), or the use of the 430:410 nm absorption ratio (Moss 1967a,b), have enabled chlorophyll *a* and phaeopigments to be estimated separately.

Acetone is not always efficient at extracting photosynthetic pigments from algae, especially Chlorophyceae and Cyanophyceae (Marker 1972, Rai 1973, Nusch & Palme 1975). Thus, methanol is sometimes used as an alternative as its extraction efficiency is superior (Marker 1972, Tett *et al.* 1975, 1977, Riemann 1980, Marker *et al.* 1980a,b). However, the absorption spectra changes upon acidification when correcting for phaeopigments (Livingston *et al.* 1953, Marker 1977, Nusch 1980) and methanol is a hazardous (and expensive) substance to work with (Marker *et al.* 1980a, Nusch 1980). This has resulted in ethanol being investigated as an alternative.

The efficiency of extraction of algal pigments with ethanol is equal to or greater than that with acetone or methanol (Moed & Hallegraff 1978, Nusch 1980, Sartory & Grobbelaar 1984, Hansson 1988), particularly if heated to its boiling point (Nusch 1980, Sartory & Grobbelaar 1984, Jespersen & Christoffersen 1987).

Most studies of algal pigment extraction with ethanol have involved plankton (e.g., Nusch 1980, Marker *et al.* 1980b, Riemann & Ernst 1982, Sartory & Grobbelaar 1984, Jespersen & Christoffersen 1987), and indeed only Tett *et al.* (1975) and Biggs (1987) has investigated extraction of pigments from benthic periphyton, and only Biggs (1987) used ethanol as the extraction solvent.

With benthic samples, no filtering or grinding of algae is usually carried out, but otherwise methods developed for plankton have been used successfully (Biggs 1987). Phytoplankton samples have been extracted in ethanol for various lengths of time by different workers (e.g., 24 h by Sartory & Grobbelaar (1984), 6,12,18,24 h by Jespersen & Christofersen (1987), 15-20 h and 24 h by Hansson (1988)), but optimal extraction times for benthic periphyton have not been determined.

In this study, I investigated the efficiency of extraction of chlorophyll *a* from various benthic algal populations to determine whether an optimal extraction regime existed. Although Biggs (1989) has established that chlorophyll *a* is stable in ethanol for up to 4 days, the stability of this molecule over a prolonged boiling period is unknown. In addition, although boiling increases quantities of algal pigments extracted, no studies have investigated the minimum incubation time required following the initial boiling step.

I was thus interested in the stability of commercially available purified chlorophyll *a*, and chlorophyll *a* extracted from natural benthic algae, and wanted to establish whether the common practice of a 24 h incubation period is really necessary for enhanced pigment extraction.

MATERIALS AND METHODS

1. Analytical procedures

The stability in 90% ethanol of chlorophyll *a* from three sources was investigated: a), commercially available purified chlorophyll from *Anacystis nidulans* (Sigma Chemicals); b), naturally occurring benthic algae; c), algae colonizing artificial substrata. Although Jespersen & Christoffersen (1987) recommended ethanol with as low a water content as possible for planktonic algae, 90% ethanol was chosen for all trials as Sartory & Grobbelaar (1984) found that more chlorophyll was extracted by 90% than 95% ethanol. The use of 90% ethanol also minimises the pH drop during acidification (Moed & Hallegraff 1978) and therefore reduces the likelihood of possible pH induced changes in absorption spectra.

a) Purified chlorophyll

A purified chlorophyll *a* solution was prepared by dissolving 1 mg of commercially available product in 90% ethanol in the dark at 5°C to give final concentrations of 100 ug l^{-1}. For manipulative work, five 100 ml. subsamples of this solution was placed in conical flasks and sealed with PVC plastic film to minimize evaporative losses. Some flasks were placed in a water bath at 83°C whereas others acted as controls (details below).

b) Natural periphyton

Stones (<10 cm diameter) covered with either the filamentous green alga *Ulothrix zonata*, and/or dominated by the diatom *Diatoma hiemale* var *mesodon*, were collected from the upper reaches of the Waimakariri River at Klondyke Corner, Arthur's Pass National Park, (South Island, New Zealand), and transported on ice to Christchurch.

Three experiments were performed with this material: experiment 1 used five *Ulothrix* covered stones; experiments 2 and 3 used five *Diatoma* covered stones. Single stones were placed in each of five 500 ml. Pyrex evaporating dishes and covered with 90% ethanol (350-500 ml.). The dishes were sealed with plastic film and placed in a water bath at 83°C for 10 minutes. Stone surface areas were determined following extraction by wrapping them in a monolayer of aluminium foil, weighing the foil and calculating the surface area from a regression curve relating foil weight to surface area.

c) Artificial substrata

The second field population of periphyton was collected on artificial substrata (unglazed red brick tiles, 10 cm x 10 cm, with and without a covering of artificial plastic turf (i.e. "grass carpet")) incubated for two months in two small alpine streams within Arthur's Pass National Park. They were heavily colonized by diatoms, predominantly *Diatoma hiemale* var *mesodon*. Seven trials were conducted, 3 with plain tiles and 4 with grass carpet covered tiles. Five substrates were used in each trial.

d) Analysis

Five millilitre subsamples were withdrawn from each solution immediately after extraction and passed through Whatman GF/C filters under vacuum. Spectrophotometric readings (665 and 750 nm) were made on a Kontron Uvikon 800 spectrophotometer (1 cm curvet) before and after acidification (Lorenzen 1967). Extracts were acidified with 0.07 ml. of 0.5M HCl and left for 30 minutes before re-reading. When the 750 nm absorbance reading exceeded 0.005, the sample was centrifuged (5 minutes at 18 400 *g*) and re-read. Absorbances of all samples from all trials were used to calculate chlorophyll *a* and phaeopigment concentrations as described by Sartory & Grobbelaar 1984).

2. Effect of Acidification

To determine whether the chlorophyll spectrum changed with pH, absorption spectra of extracts before and after acidification were plotted, and maximum absorption values in the 660-670 nm region compared. The efficiency of conversion of chlorophyll to phaeopigment by the addition of acid was also assessed by comparing experimentally observed acid ratios to the "standard" phytoplankton derived acid ratio of 1.72 (Sartory & Grobbelaar 1984).

3. Effect of Boiling

The stability of chlorophyll *a* in boiling (83°C) 90% ethanol was determined using large subsamples of the 100 ug l^{-1} stock solution and extracts from the river populations. Each was boiled in a sealed container for 45 minutes and aliquots (5 ml) were withdrawn at intervals, cooled, filtered and analysed as described above.

4. Effect of Extraction Time

Stability of chlorophyll *a* in ethanol was examined during a 24 h pigment extraction period by boiling five 100 ml subsamples of the 120 ug l^{-1} stock solution for 10 minutes, and then incubating them for up to 24 hours in the dark at 5°C. Five millilitre subsamples were withdrawn for analysis every 2 hours. Five 100 ml unboiled samples of each stock solution served as controls.

Stability of algal pigments extracted from natural populations of Ulothrix and *Diatoma*, and from the seven trials using artificial substrates, was examined during a 24

hour period at 5°C in the dark following initial extraction for 10 minutes in boiling ethanol (83°C). Throughout the 24 hour period, extracts were gently shaken to ensure constant mixing of solutions. Subsamples for spectrophotometric analysis were withdrawn every 2 hours.

5. Statistical Analysis

The objective of this study was to determine whether calculated concentrations of chlorophyll *a* and phaeopigments varied over a 24 h incubation period. I was most interested in assessing the extent of variability among readings, and therefore percentage changes in calculated pigment concentrations were compared with initial values. Differences in percentage change over time among samples were analysed by 2-Way ANOVA after it had been demonstrated that each time interval was independent of the previous one by a time-series analysis.

Relationships between percentage change of chlorophyll *a*, phaeopigments and total pigments (chlorophyll *a* + phaeopigments), and time, were assessed by multiple regression analysis to determine whether fluctuations were predictable over time. In addition, the "acid ratio" of chlorophyll *a* extracted from replicate samples in each experiment was determined by calculating the regression between absorbances before and after acidification.

RESULTS

1. Effect of Acidification

The pH of extracts dropped from 8.1 before to 3.6 after acidification. Absorption spectra of extracts following this pH drop showed no discernible shift and the peak remained at 665 nm (Fig 1). Highly significant correlations existed between absorbance readings before and after acidification, indicating that phaeophytinization had occurred. Preliminary studies also revealed that this was complete within 5-10 minutes of the addition of 0.5 ml HCl, whereas with weaker acids it was not complete even after 1 hour (Fig 2).

Acid ratios calculated for the solution of commercially prepared chlorophyll were close to those previously reported (i.e., 1.72; Sartory & Grobbelaar 1984), but those from the chlorophyll *a* extracted from natural algal populations were often considerably less than this (Table 1). Combining data from all trials with algae from the field, I obtained a mean acid ratio of 1.53.

2. Effect of Boiling

Boiling the 100 ug l^{-1} stock solution at 83°C resulted in no significant changes in either chlorophyll *a* or phaeopigment concentration after 45 minutes ($F = 1.19, 2.03$; $p>0.05$; Fig. 3).

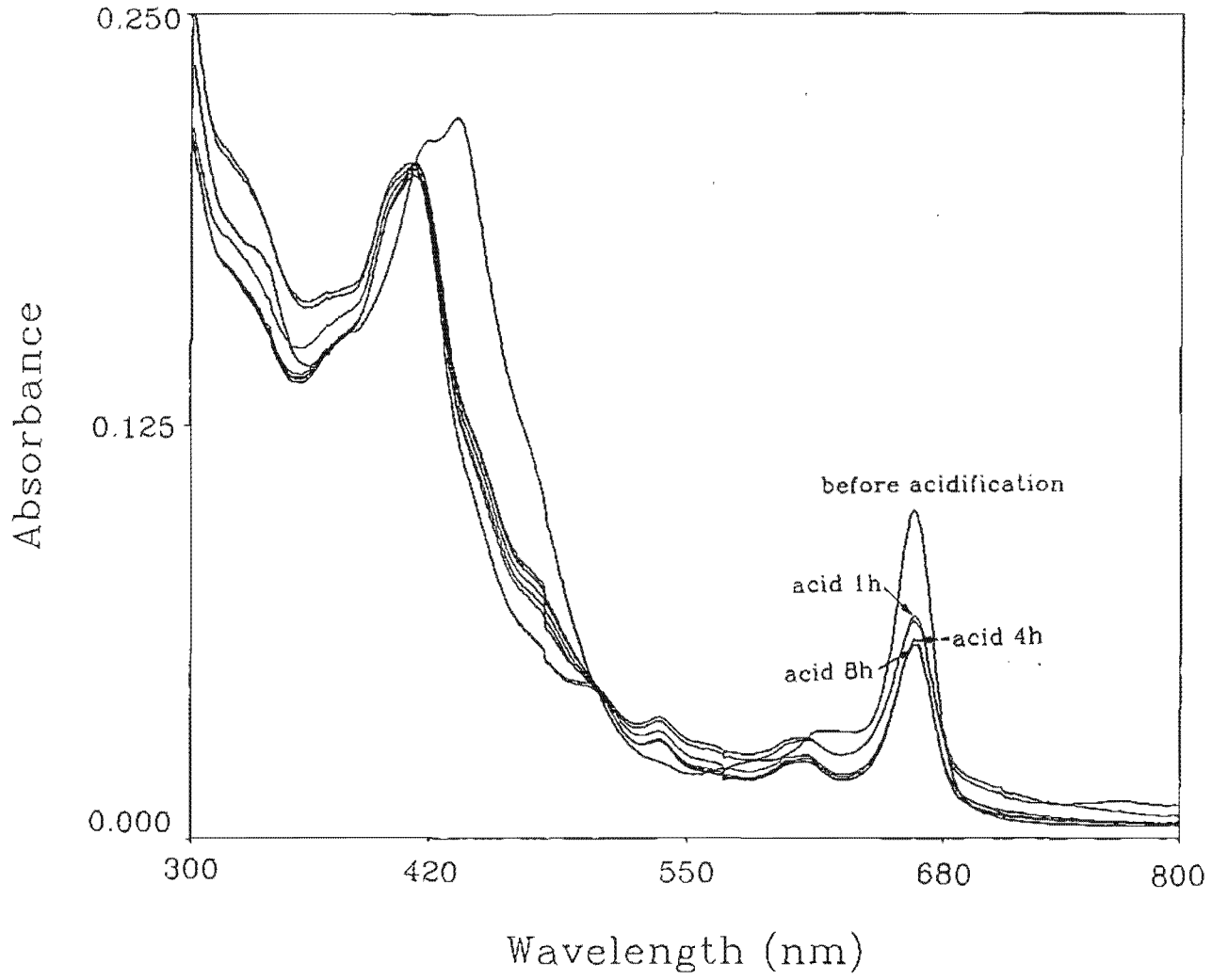


Fig 1: Absorption spectra of chlorophyll *a* extracts in 90% ethanol before acidification with 0.07 ml of 0.5 M HCl, and at 1, 2, 4, and 8 hours after acidification. .

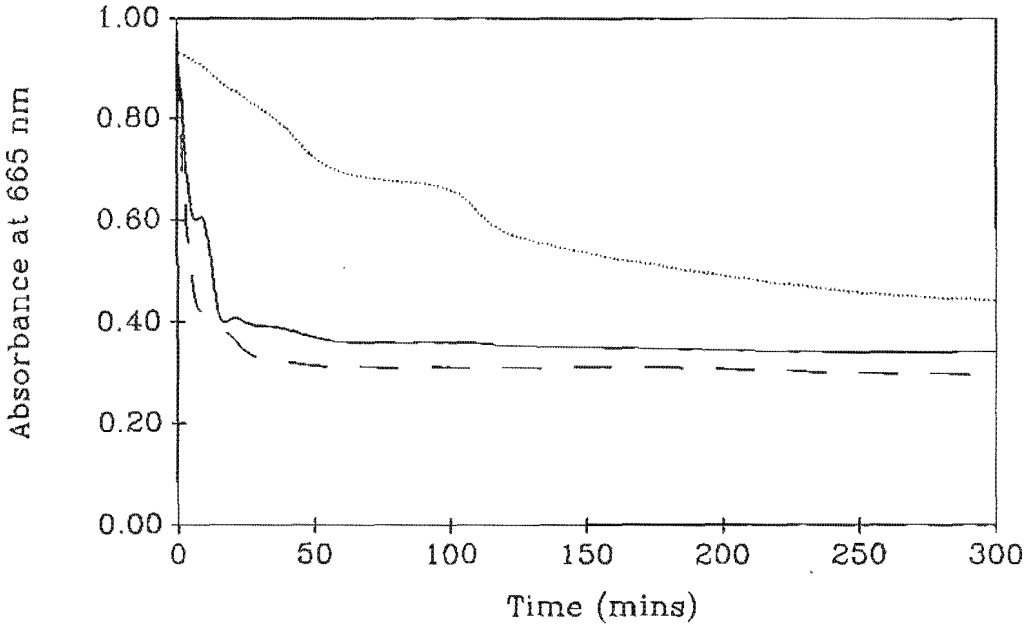


Fig 2: Effect of increasing acid concentration on the speed of phaeophytinization of chlorophyll *a* in 90% ethanol, showing the decrease in absorbance at 665 nm following addition of various strengths of HCl. Dotted line = 0.025 M HCl; dashed line = 0.1 M HCl; Solid line = 0.5 M HCl.

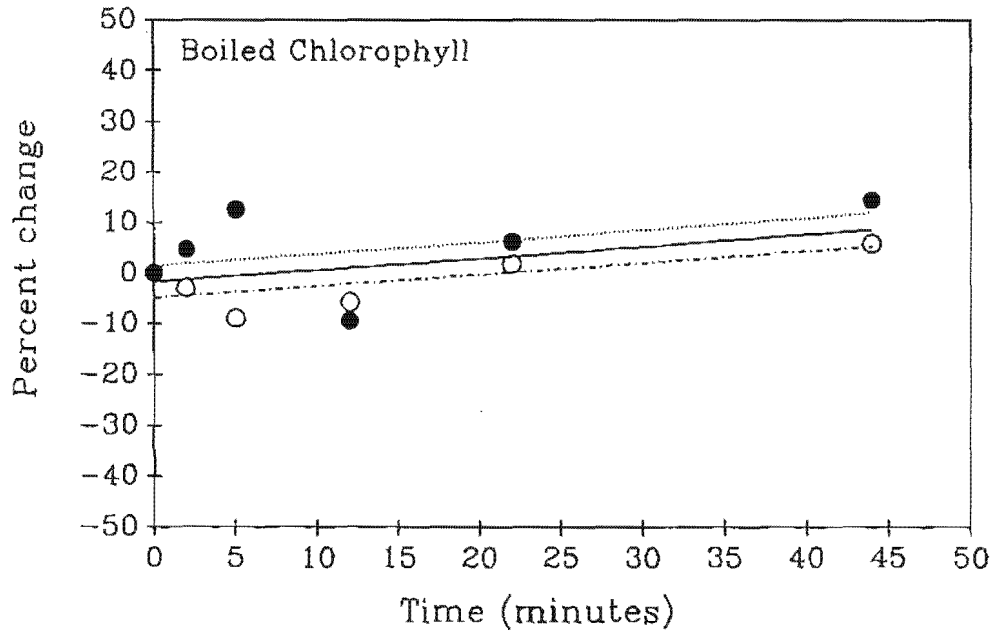


Fig 3: Percent change in chlorophyll *a* and phaeopigment concentrations in a 100 ug l^{-1} stock solution of chlorophyll *a* boiled for increasing lengths of time at 83°C in 90% ethanol. Open symbols = percent change in chlorophyll *a* concentrations; closed symbols = percent change in phaeopigment concentrations; (mean values only shown, n = 5). Calculated regression lines of chlorophyll *a* (dashed line), phaeopigments (dotted line) and total pigment concentrations (solid line) over time are also shown.

Table 1: List of acid ratios empirically observed in all trials conducted using chlorophyll derived from 3 sources: a) the commercially prepared chemical; b) chlorophyll extracted from natural algal communities; c) chlorophyll extracted from algae colonizing artificial substrates: either plain or carpeted tiles at both sites.

Chlorophyll Source	Assay	Acid-ratio	number of samples	r^2
a) Purefied chemical	Control chlorophyll 1	1.65	60	0.907
	Boiled chlorophyll 1	1.68	60	0.944
b) Natural periphyton	Ulothrix	1.47	78	0.905
	Diatoma 1	0.854	65	0.889
	Diatoma 2	0.647	78	0.863
c) Artificial substrata	a) Mouse Stream (carpet)	1.68	65	0.985
	b) Mouse Stream (carpet)	1.64	65	0.983
	c) Tim's Creek (carpet)	1.71	65	0.940
	d) Tim's Creek (carpet)	1.57	65	0.868
	e) Mouse Stream (tile)	1.33	65	0.987
	f) Mouse Stream (tile)	1.19	66	0.935
	g) Tim's Creek (tile)	1.29	54	0.935
	TOTAL DATA SET (excluding purefied chlorophyll)	1.528	666	0.961

Increased boiling of periphytic *Ulothrix* and *Diatoma* samples in ethanol resulted in enhanced chlorophyll *a* extraction (r^2=0.406, Ulothrix; r^2 = 0.362, Diatoma, p<0.001) and absorbances read after 20 minutes boiling were significantly higher than those extracted after two minutes (F=37.96, Ulothrix; F=50.66, Diatoma; p<0.01). Although chlorophyll *a* extraction was enhanced, boiling resulted in no increase in phaeopigment concentrations (Figs 4a,b).

3. Effect of Extraction Time

a) Stock solutions

The percentage change in chlorophyll *a* concentration varied significantly over the 24 h period in both the unboiled (control) 100 ug l^{-1} chlorophyll solution and in the chlorophyll solution that had been boiled for 10 minutes (F= 9.31 control, F= 20.65 boiled; p<0.001). Although chlorophyll *a* concentration in the control solution was significantly and negatively correlated with length of incubation time, total pigment concentrations displayed no such relationship (Fig. 5; Table 2a,b).

Calculated phaeopigment values also varied significantly over time (F= 5.00 control, F= 20.7 boiled; p<0.001, Fig 5), but no significant correlations between phaeopigment concentrations and incubation time were observed (Table 2c).

b) Stone communities

The apparent concentration of chlorophyll *a* extracted from periphytic communities dominated by *Ulothrix* and *Diatoma* (trial 1) fluctuated significantly over time (F=7.41 *Ulothrix*, F=3.79 *Diatoma*, p<0.001). No significant correlations existed between concentrations of either chlorophyll *a* or total pigment concentration and incubation time (Table 2a,b), and no pattern was observed in these fluctuations (Figs 6a,b).

Phaeopigment concentrations also fluctuated over time in samples extracted from *Diatoma* communities in Trial 1 (F=7.3, p<0.001, Fig 7b) but no significant differences were observed in phaeopigment concentrations extracted from *Ulothrix* (F=0.71, p>0.05; Fig 6a). No trends were observed between phaeopigment concentrations and time (Table 2c).

In the second trial, chlorophyll *a* and phaeopigment concentrations in extracts from Diatoma did not differ significantly with time (F=1.44, chlorophyll *a*; F=1.38, phaeopigment; p>0.05; Fig 6c, Table 2 a,b,c).

c) Artificial substrate communities

Chlorophyll *a* concentrations in extracts from algae grown on artificial substrata varied significantly with time in 6 of the 7 trials analysed (F= 3.25, 4.76, 3.40, 44.1, 5.5, 9.5; for trials a, b, c, d, e, f respectively; p<0.05, Fig 7 a-g). Variations in chlorophyll *a* concentration were not correlated with time and followed no consistent patterns and total pigment concentration was only correlated to time on 3 occasions (Table 2 a,b).

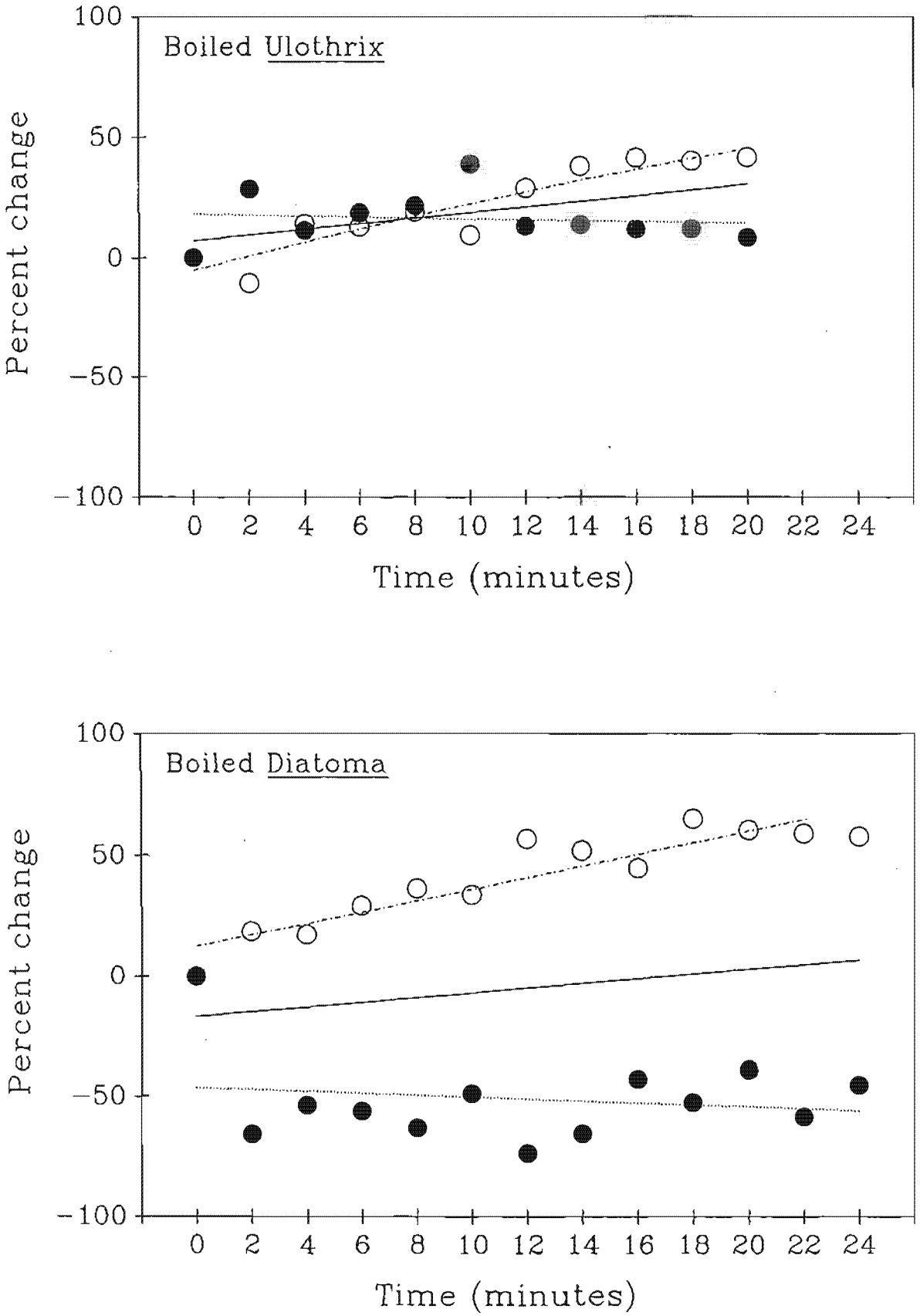


Fig 4: Percent change in concentrations of chlorophyll *a*, phaeopigment and total pigment extracted from natural periphyton assemblages boiled for increasing lengths of time at 83°C in 90% ethanol. a, *Ulothrix* dominated periphyton; b, *Diatoma* dominant. Conventions as per Fig.3.

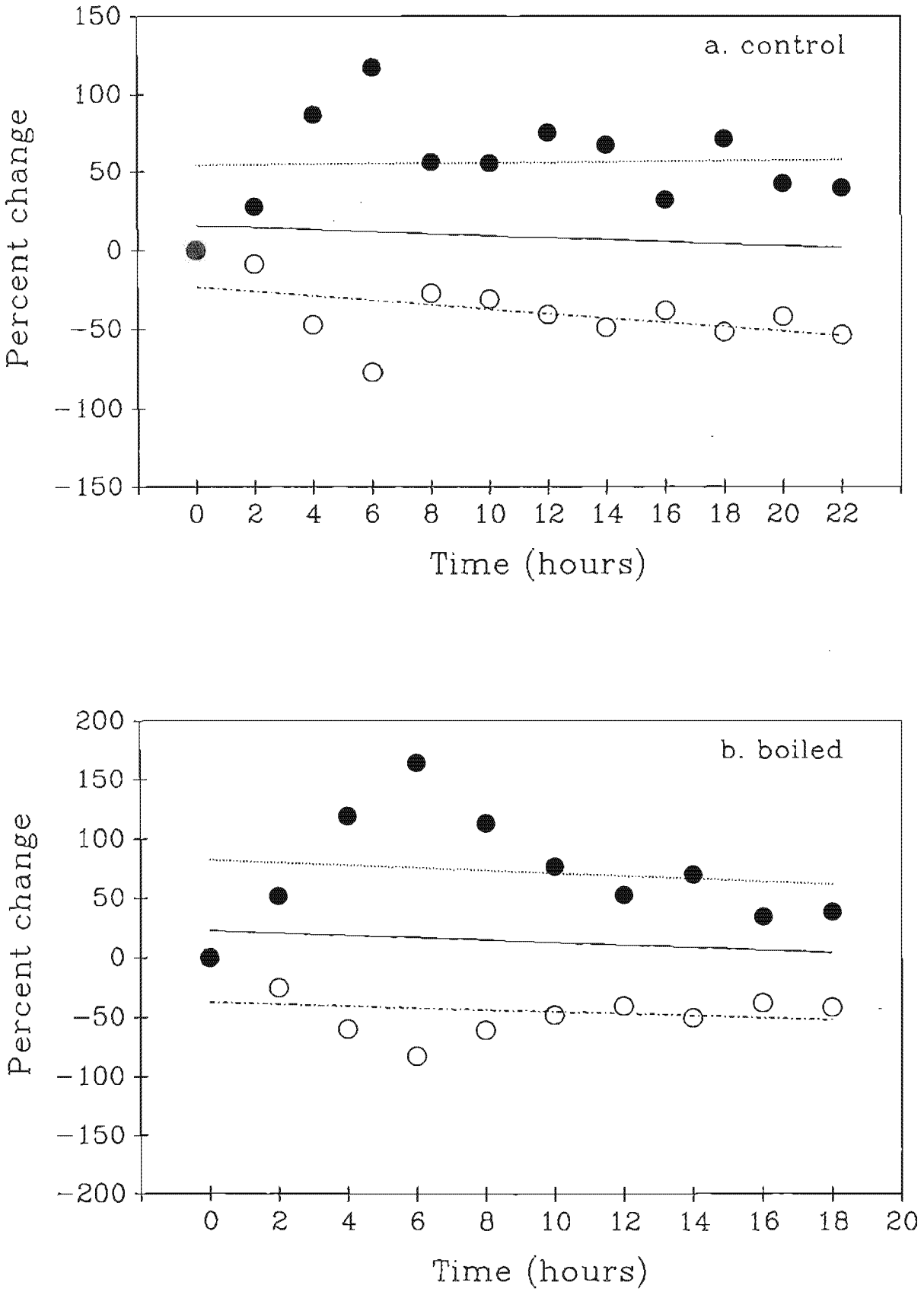


Fig. 5: Percent change in concentrations of chlorophyll *a*, phaeopigment and total pigment concentrations in a stock solution made up to an initial chlorophyll *a* concentration of 100 ug l^{-1} and left steeping for increasing lenghts of time in 90% ethanol. Conventions as per Fig. 3.

Table 2: Regression coefficients relating percentage change in pigment concentration to extraction time of chlorophyll from three sources. These regressions express the equation: % change = A x time + C. Those equations showing a significant relationship (p <0.05) between chlorophyll *a* concentration and time are indicated by *. 2a = chlorophyll *a* concentration; 2b = total pigment concentration; 2c = phaeopigment concentration.

2a) Chlorophyll a

Chlorophyll Source	Assay	slope (A)	constant (C)	r2	P
a) Purefied chemical	Control chlorophyll 1	-2.861	-20.18	0.109	0.003*
	Boiled chlorophyll 1	-1.69	-35.3	0.043	0.126
b) Natural periphyton	Ulothrix	-0.573	0.900	0.015	0.392
	Diatoma 1	1.24	-19.5	0.014	0.454
	Diatoma 2	-0.503	10.35	0.009	0.553
c) Artifical substrata	a) Mouse Stream (carpet)	0.084	29.03	0.022	0.323
	b) Mouse Stream (carpet)	-0.524	40.26	0.016	0.388
	c) Tim's Creek (carpet)	-0.024	24.93	0	0.999
	d) Tim's Creek (carpet)	-0.758	0.863	0.032	0.161
	e) Mouse Stream (tile)	-2.05	-53.7	0.066	0.036*
	f) Mouse Stream (tile)	-0.624	3.44	0.005	0.733
	g) Tim's Creek (title)	0.864	-15.94	0.009	0.644

2b) **Total Pigment Concentration**

Chlorophyll Source	Assay	slope (a)	constant (c)	r2	P
a) Purified chemical	Control chlorophyll 1	-0.304	-40.5	0.001	0.895
	Boiled chlorophyll 1	-1.012	-22.72	0.007	0.521
b) Natural periphyton	Ulothrix	-0.109	-5.968	0.001	0.936
	Diatoma 1	-0.109	-3.42	0.001	0.757
	Diatoma 2	0.817	3.55	0.006	0.456
c) Artifical substrata	a) Mouse Stream (carpet)	-0546	16.29	0.007	0.477
	b) Mouse Stream (carpet)	-1.345	26.35	0.059	0.006*
	c) Tim's Creek (carpet)	-0.866	15.48	0.017	0.149
	d) Tim's Creek (carpet)	-1.446	1.227	0.088	0.001*
	e) Mouse Stream (tile)	-1.26	-27.32	0.059	0.003*
	f) Mouse Stream (tile)	-1.183	43.80	0.0143	0.154
	g) Tim's Creek (title)	-1.017	1.989	0.004	0.713

2c Phaeopigments

Chlorophyll Source	Assay	slope (a)	constant (c)	r2	P
a) Purefied chemical	Control chlorophyll 1	1.599	-59.4	0.003	0.869
	Boiled chlorophyll 1	-2.35	84.8	0.017	0.439
b) Natural periphyton	Ulothrix	0.133	-12.39	0	0.984
	Diatoma 1	0.349	26.22	0.001	0.908
	Diatoma 2	0.065	-16.76	0	0.987
c) Artificial substrate	a) Mouse Stream (carpet)	-1.69	-2.91	0.111	0.001*
	b) Mouse Stream (carpet)	-2.116	11.94	0.190	0.001*
	c) Tim's Creek (carpet)	-1.91	8.53	0.120	0.001*
	d) Tim's Creek (carpet)	-2.09	1.457	0.159	0.001*
	e) Mouse Stream (tile)	-2.988	4.072	0.154	0.001*
	f) Mouse Stream (tile)	-4.11	88.89	0.034	0.111
	g) Tim's Creek (title)	-5.125	25.604	0.011	0.615

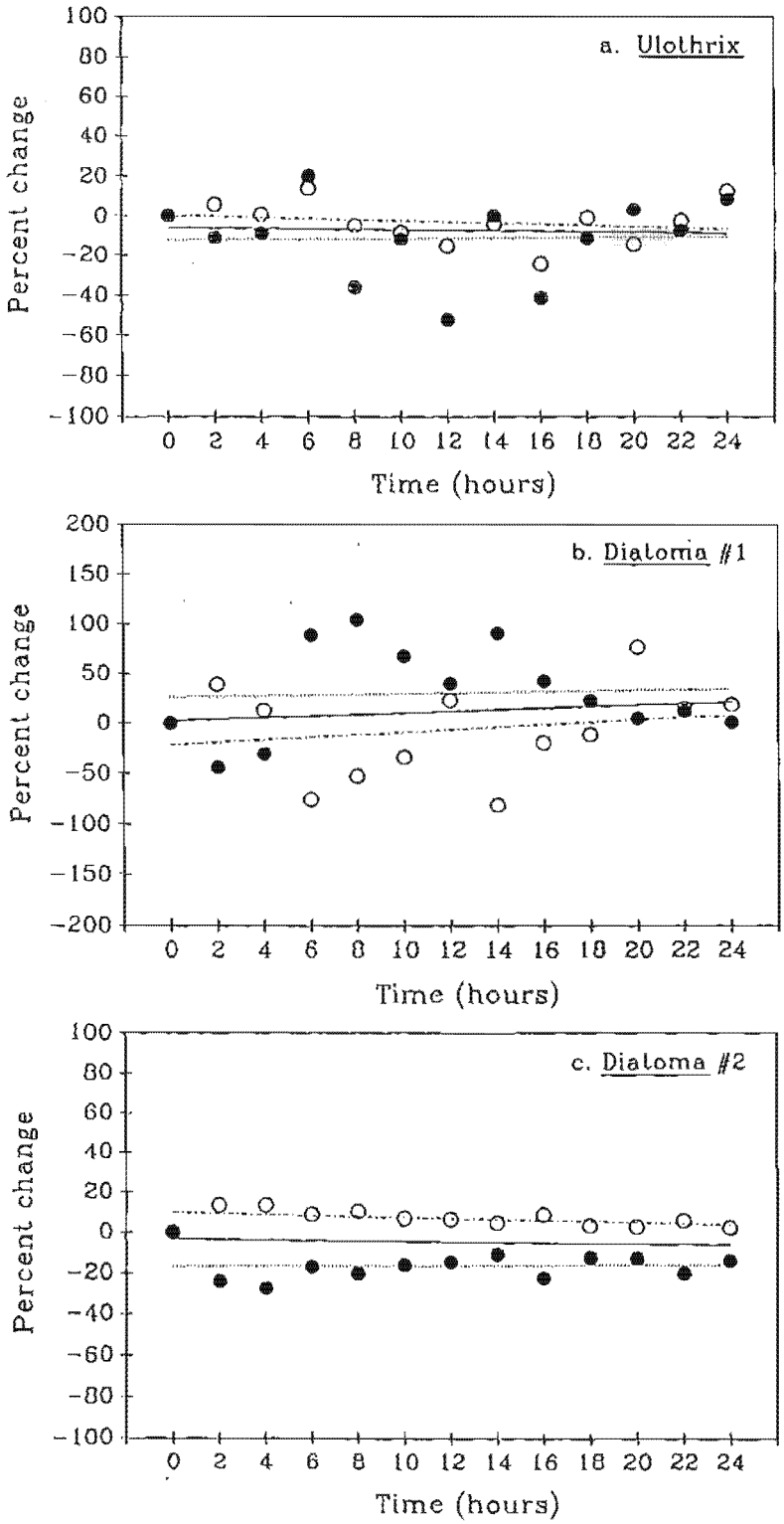


Fig. 6: Percent change in concentrations of chlorophyll *a*, phaeopigment and total pigment extracted from natural periphyton assemblages steeped for increasing lengths of time in 90% ethanol. a, *Ulothrix* dominated periphyton, b, *Diatoma* dominant. Conventions as per Fig.3.

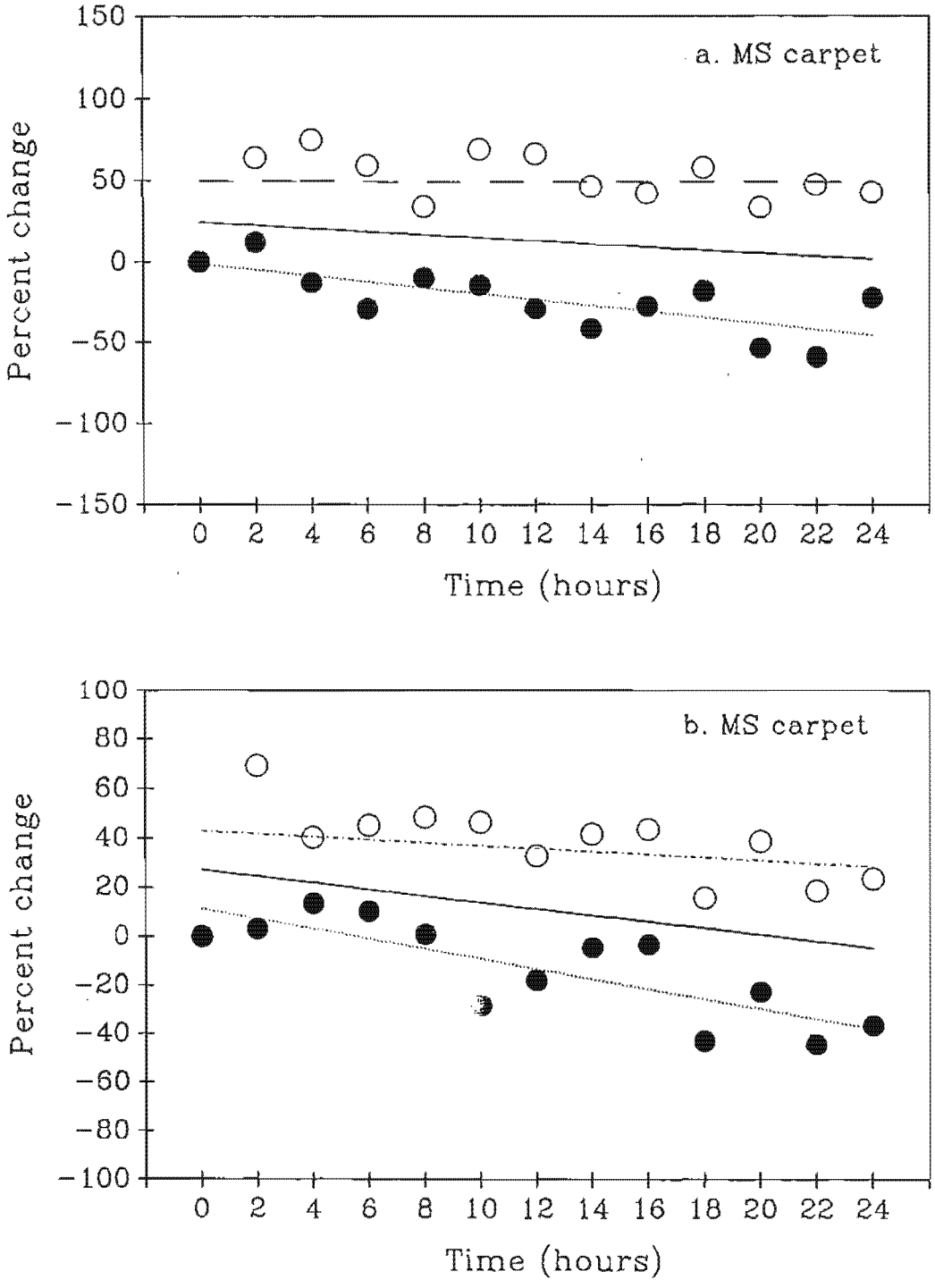
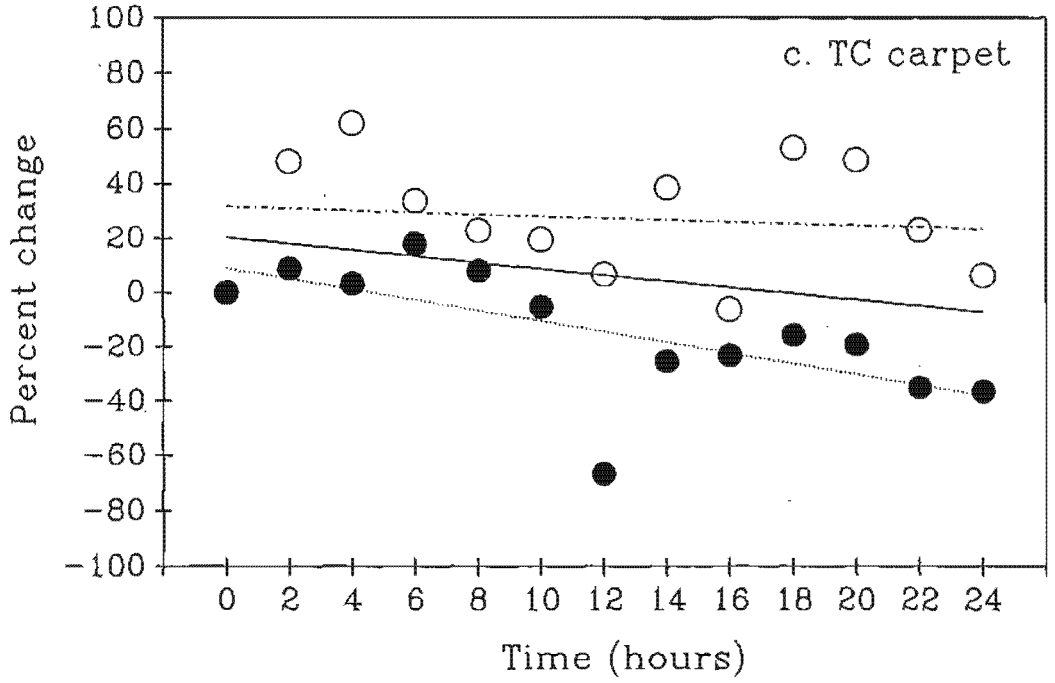
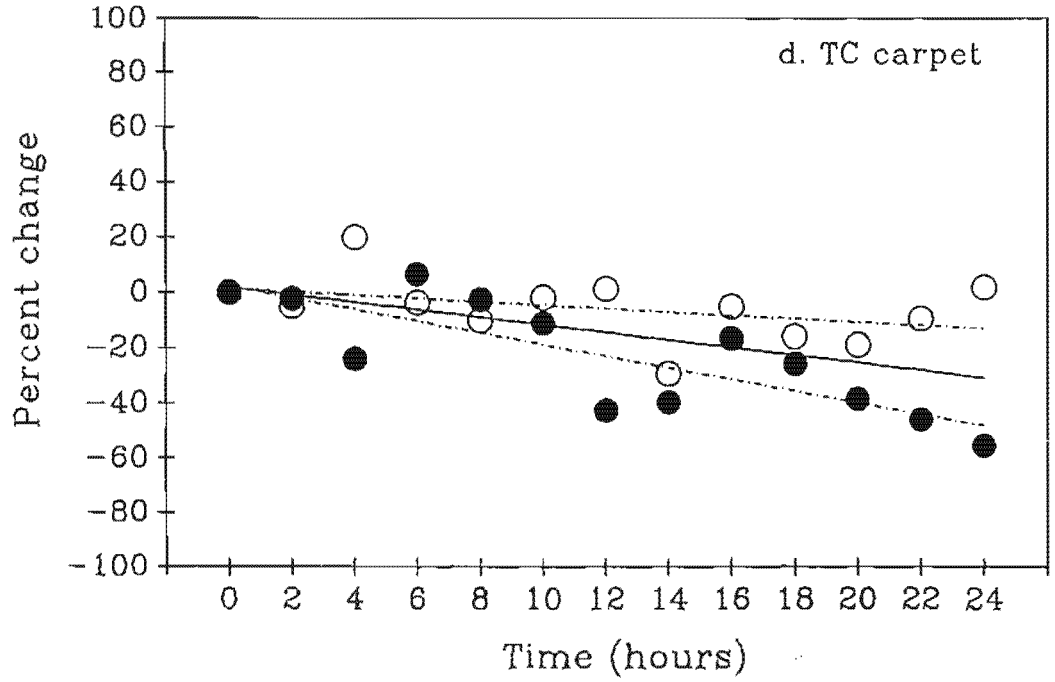
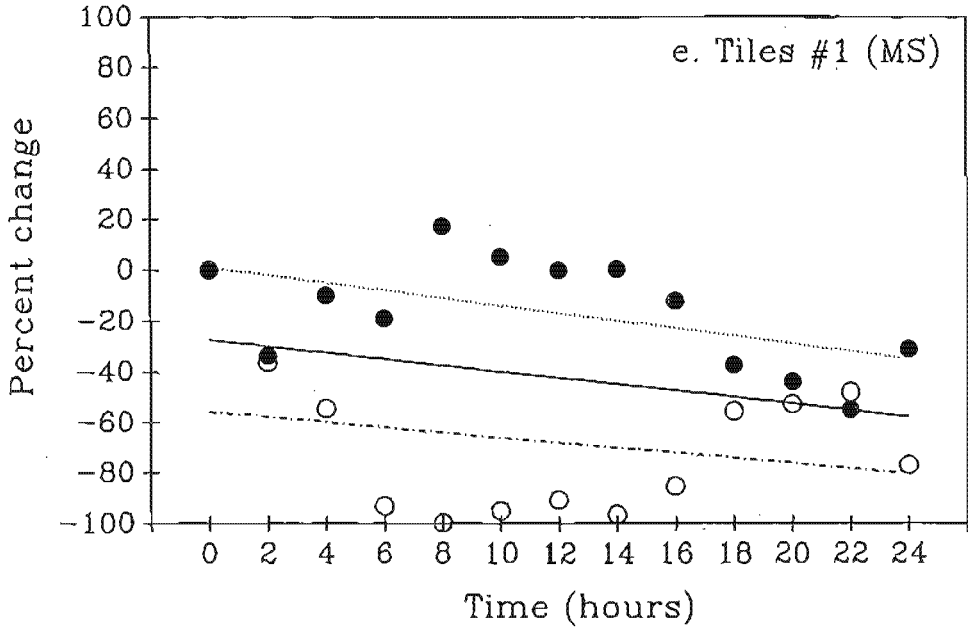
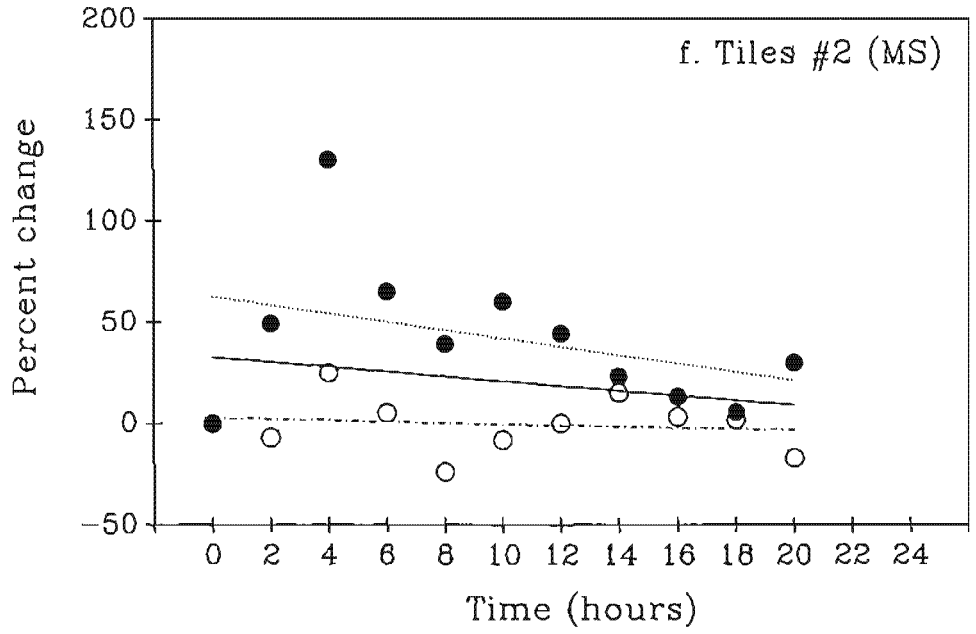


Fig. 7: Percent change in concentrations of chlorophyll *a*, phaeopigments and total pigments extracted from algae colonising artificial substrata placed for 2 months in small alpine streams. Extracts were steeped for increasing lengths of time in 90% ethanol. a - d, carpet covered tiles at Mouse Stream (MS) and Tim's Creek (TC); e - g; plain tiles at Mouse Stream and Tim's Creek. Conventions as per Fig.3.


c. TC carpet
Percent change
100
80
60
40
20
0
-20
-40
-60
-80
-100
0 2 4 6 8 10 12 14 16 18 20 22 24
Time (hours)


d. TC carpet
Percent change
100
80
60
40
20
0
-20
-40
-60
-80
-100
0 2 4 6 8 10 12 14 16 18 20 22 24
Time (hours)


e. Tiles #1 (MS)
Percent change
100
80
60
40
20
0
-20
-40
-60
-80
-100
0 2 4 6 8 10 12 14 16 18 20 22 24
Time (hours)


f. Tiles #2 (MS)
Percent change
200
150
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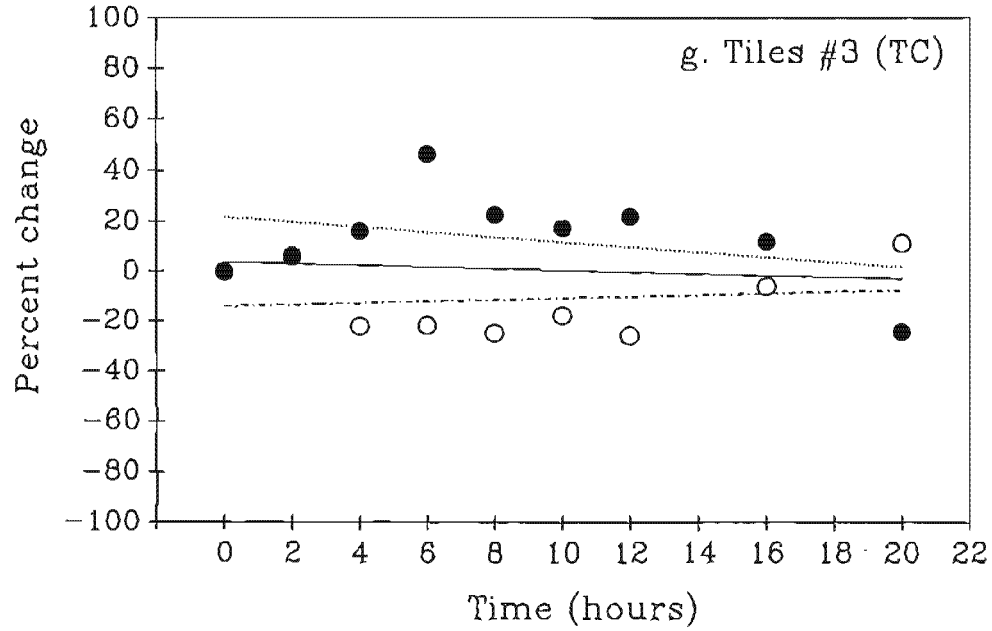
Time (hours)


g. Tiles #3 (TC)
Percent change
100
80
60
40
20
0
-20
-40
-60
-80
-100
0 2 4 6 8 10 12 14 16 18 20 22
Time (hours)

Calculated phaeopigment values also varied significantly with time in 6 of the 7 trials conducted ($F=2.26, 3.59, 5.40, 3.90, 4.42, 7.15$ for trials 1 to 6 respectively; $p<0.05$, Fig 10 a-g), and in contrast with chlorophyll *a* values were significantly and negatively correlated with time (Table 2c).

DISCUSSION

1. Effect of Boiling

The absence of a marked increase in phaeopigment in extracts of purified chlorophyll *a* boiled for up to 45 minutes indicates that chlorophyll *a* was stable in boiling ethanol for at least that length of time. These results confirm those obtained by Sartory & Grobbelaar (1984) who found that phaeopigment was formed in ethanol only after 30 minutes at 78°C.

Although boiling algal samples in ethanol improves extraction efficiency of chlorophyll *a* (Nusch 1980, Sartory & Grobbelaar 1984, Jespersen & Christoffersen 1987), no optimal boiling time for benthic algae has been suggested. I found that extraction of chlorophyll *a* from *Ulothrix* and *Diatoma* increased with boiling for 16 and 12 minutes, respectively, and during this time no increases in phaeopigment occurred. Differences between the two algae may reflect the ease with which the chlorophyll *a* molecule can leave their cells, and suggests that optimal boiling times are likely to be species specific. It was apparent, however, that boiling for only 5 minutes as recommended by Sartory & Grobbelaar (1984) and Jespersen & Christoffersen (1987) would have resulted in under-estimates of the chlorophyll *a* content of the periphytic algae used in the present study.

2. Effect of Acidification

The acidification procedures of Lorenzen (1967) and Moss (1967 a,b) were designed to discriminate between chlorophyll and phaeopigments, and assume that the red absorption maximum of phaeopigments after acidification is the same as the pre-acidification peak. Although Livingstone *et al.* (1953) and Marker (1977) showed that the phaeopigment spectrum can be highly sensitive to pH changes in methanol and acetone, no spectral shift occurred in any of the samples I processed in ethanol (e.g., Fig 1). This supports the observations of Moed & Hallegraff (1978) and Nusch (1980) that ethanol is more satisfactory than methanol and acetone for determining phaeopigment concentrations in algal extracts.

The final concentration of acid added to my extracts to convert chlorophyll to phaeopigment was 7×10^{-3}M, stronger than the 4×10^{-3}M recommended by Moed & Hallegraff (1978) to prevent formation of interfering phaeopigment di-cations. Nevertheless, the final pH of my solutions (3.6) was higher than that recommended by them (2.6-2.8). Whereas conversion of chlorophyll *a* to phaeopigment is sometimes slow when acidification is carried out with weak acids (Marker & Jinks 1982) or at pH>2.8

(Moed & Hallegraff 1978), phaeophytinization was always complete within 5-10 minutes in my study.

The significant relationship between absorbances of pre- and post-acidified chlorophyll extracts supports the assumption that phaeophytinization had occurred, but the ratio between pre- and post-acidified chlorophyll readings from pigments extracted from natural algal populations was always lower than the value of 1.72 given by Sartory & Grobbelaar (1984). However, they derived this ratio from empirical studies with purified chlorophyll *a* extracted from planktonic algae, and the lower ratio I obtained therefore reflects the presence of phaeopigments in the natural periphytic communities used in this study.

3. Effect of Incubation

Results of all trials showed that concentrations of chlorophyll *a* and phaeopigments fluctuated significantly over time. Nevertheless, these fluctuations were of an unpredictable nature and no time dependent trends were evident. My results indicate that boiling, and not subsequent incubation is of greatest importance for removing the chlorophyll *a* molecule from natural algal populations. Moreover, I demonstrated that it is certainly not necessary to incubate extracts for 24 hours, as pigment concentrations within this period appear to be independent of the length of incubation time.

These results of this study are consistent with those of Biggs (1987) who found little change in chlorophyll *a* concentration of benthic algal extracts for up to 4 days following extraction. They also have important methodological implications. Thus my results suggest that boiling times required to maximise chlorophyll *a* extraction may be species specific. Furthermore, it is unnecessary to leave samples steeping in ethanol for 24 h as boiling is responsible for the extraction of almost all algal pigments from benthic algae.

REFERENCES.

Biggs, B.J.F. (1987). Effects of sample storage and mechanical blending on the quantitative analysis of river periphyton. *Freshwat.Biol.* 18: 197-203.

Hansson, L.A. (1988). Chlorophyll *a* determination of periphyton on sediments: identification of problems and recommendation of method. *Freshwat.Biol.* 20: 347-352.

Jespersen, A-M., & Christoffersen, K. (1987). Measurements of chlorophyll *a* from phytoplankton using ethanol as extraction solvent. *Arch.Hydrobiol.* 109: 445-454.

Livingston, R., Parlser, R., Thomposn, L., & Weller, A. (1953). Absorption spectra of solutions of phaeophytin *a* in methanol containing acid or base. *J.Am.Chem.Soc.* 75: 3025-3026.

Lorenzen, C.J. (1967). Determination of chlorophyll and phaeopigments: spectrophotometric equations. *Limnol.Oceanogr.* 12: 343-346.

Marker, A.F.H. (1972). The use of acetone and methanol in the estimation of chlorophyll in the presence of phaeophytin. *Freshwat.Biol.* 2: 361-385.

Marker, A.F.H. (1977). Some problems arising from the estimation of chlorophyll *a* and phaeophytin *a* in methanol. *Limnol.Oceanogr.* 22: 578-579.

Marker, A.F.H., Crowther, C.A. & Gunn, R.J.M. (1980a). Methanol and acetone as solvents for estimating chlorophyll *a* and phaeopigments by spectrophotometry. *Arch.Hydrobiol.Beih. Ergebn.Limnol.* 14: 52-69.

Marker, A.F.H., Nusch, E.A., Ral, H., & Riemann, B. (1980b). The measurement of photosynthetic pigments in freshwaters and standardization of methods: Conclusions and recommendations. *Arch.Hydrobiol.Beih.Ergebn.Limnol.* 14: 91-106.

Marker, A.F.H., & Jinks, S. (1982). The spectrophotometric analysis of chlorophyll *a* and phaeopigments in acetone, ethanol ans methanol. *Arch.Hydrobiol.Beih.Ergebn.Limnol.* 16: 3-17.

Moed, J.R., & Hallegraeff, G.M. (1978). Some problems in the estimation of chlorophyll *a* and phaeopigments from pre- and post-acidification spectrophotometric measurements. *Int.Revue.ges.Hydrobiol.* 63: 787-800.

Moss, B. (1967a). A spectrophotometric method for the estimation of percentage degradation of chlorophylls to phaeopigments in extracts of algae. *Limnol.Oceanogr.* 12: 335-340.

Moss, B. (1967b). A note on the estimation of chlorophyll *a* in freshwater algal communities. *Limnol.Oceanogr.* 12: 340-342.

Nusch, E.A., & Palme, G. (1975). Biologische Methoden für die Praxis der Gerwässeruntersuchung. *Bestimmung des Chlorophyll a- und Phaeopigmentgehaltes in Oberflächenwasser. GWF-Wasser/Abwasser* 116: 562-565.

Nusch, E.A. (1980). Comparison of different methods for chlorophyll and phaeopigment determination. *Arch.Hydrobiol.Beih. Ergebn.Limnol.* 14: 14-36.

Rai, H. (1973). Methods involving the determination of photosynthetic pigments using spectrophotometry. *Verh.Internat.Verein.Limnol.* 18: 1864-1874.

Riemann, B. (1980). A note on the use of methanol as an extraction solvent for chlorophyll *a* determination. *Arch.Hydrobiol. Beih. Ergebn.Limnol.* 14: 70-78.

Riemann, B., & Ernst, D. (1982). Extraction of chlorophylls *a* and *b* from phytoplankton using standard techniques. *Freshwat. Biol.* 12: 217-223.

Richards, F.A., & Thompson, T.G. (1952). The estimation and characterization of plankton populations by pigment analyses. I. A spectrophotometric method for the estimation of plankton pigment. *J.Mar.Res.* 11: 156-172.

Sartory, D.P., & Grobbelaar, J.U. (1984). Extraction of chlorophyll *a* from freshwater phytoplankton for spectrophotometric analysis. *Hydrobiol.* 114: 177-187.

Strickland, J.D.H., & Parsons, T.R. (1968). A practical handbook of seawater analysis. *Bull.Fish.Res.Bd.Can.* 167: 311pp.

Tett, P., Kelly, M.G., & Hornberger, G.M. (1975). A method for the spectrophotometric measurement of chlorophyll *a* and phaeophytin in benthic microalgae. *Limnol.Oceanogr.* 20: 887-896.

Tett, P., Kelly, M.G., & Hornberger, G.M. (1977). Estimation of chlorophyll a and phaeophytin a in methanol. *Limnol.Oceanogr.* 22: 579-580.

Vollenwelder, R.A. (1969). IBP Handbook No 12: A manual on methods of measuring primary production in aquatic environments. Blackwell Scient.Publ., Oxford/Edingburgh.

Wetzel, R.G. and Westlake, D.F. (1969). Periphyton, *In* Vollenwelder, R.A. *A manual on the methods of measuring primary production in aquatic environments.* Blackwell Scientific Publications, Oxford. pp. 33-40.

Wilkinson, L. (1988). SYSTAT: The system for statistics. Evanston, IL: SYSTAT, Inc. 823pp.

APPENDIX THREE:

TOXICITY OF THE INSECTICIDE/NEMATICIDE "VYDATE"

TO AQUATIC INVERTEBRATES AND NATURAL PERIPHYTIC COMMUNITIES

INTRODUCTION

As part of an investigation into invertebrate colonization of artificial mosses, it became necessary to remove all invertebrates from artificial substrata while keeping the natural periphytic communities, and trapped detrital particles intact. This enabled comparisons to be made of short term colonization between substrata with abundant algal and detrital foods and similar structures without. To remove invertebrate communities from these structures, Dr John Marshall, DSIR Plant Protection, Lincoln suggested use of the nematicide/insecticide Vydate ^{R}.

As nothing was known about the effects of Vydate on stream biota, I needed to ascertain whether Vydate would kill invertebrates potentially encountered on artificial substrata and whether it would damage the algal communities present. If algal communities were damaged by an application of Vydate, then a reduction in biomass of algae could influence subsequent invertebrate colonization patterns.

In order to determine whether algal communities were damaged by immersion in solutions of Vydate, I measured differences in pigment content (chlorophyll *a* and phaeopigments) of naturally occurring benthic algal communities following exposure to increasing concentrations of the chemical. An increase in the percentage contribution of phaeophytin to total algal pigments was used to assess cellular damage to algae.

MATERIALS AND METHODS

Fifty algae-covered cobbles were collected from the upper Waimakariri River at Klondyke Corner, Arthurs Pass National Park. They were placed in plastic bags and transported on ice to Christchurch where analysis began within 4 hours of collection. Invertebrates were collected were taken from riffles in the river and returned to the laboratory in containers of river water kept on ice. River water to be used in experiments was collected in plastic Jerry cans.

Effect on algae

Algal covered stones were divided into 5 groups of 10 stones, and each stone was placed in a separate 2 litre container. Solutions of Vydate were made up in appropriate quantities of river water to final concentrations of 5, 10, 50 and 100 ppm, and enough solution was added to each container to cover the cobbles. Cobbles in pure river water acted as no-treatment controls. Containers were placed in a 5°C constant temperature room and aerated.

After 24 hours, all cobbles were removed from each solution and placed in 90% ethanol. Pigments were extracted after boiling samples (83°C) for 10 minutes and incubating for 2 hours (Appendix 2). Subsamples were withdrawn from each sample and following filtration through Whatman GFC paper to remove particulates, absorbances were read at 665 nm and 750 nm. After acidification (0.5M HCl, 1h) absorbances were reread and chlorophyll and phaeopigment values calculated. All

cobbles were subsequently washed free of algal material and wrapped tightly in a mono-layer of aluminium foil which was cut to size, removed and weighed. Weights were converted to surface areas using a weight-area curve and pigment values were expressed as $\mu g\ cm^{-2}$ of stone surface.

Effect on invertebrates

All invertebrates collected were sorted into taxa which were placed separately into containers containing the same concentrations of Vydate as used in the trials with algae. Taxa used were *Deleatidium* (10 individuals per container), *Hydrobiosis* sp. (3 individuals per container), *Limonia hudsoni* (5 individuals per container) *Olinga feredayi* (4 individuals per container), *Zelandoperla* (4 individuals per container), and Chironomidae (25 individuals per container). Triplicate containers of invertebrates were used for each Vydate concentration. All experimentals were conducted at constant temperature (5°C) with continuous, gentle aeration. Invertebrates placed in river water alone acted as controls. After a 24h exposure period, the number of animals alive was recorded, and percentage mortality in each solution was calculated.

Effect of time exposed

Following selection of a suitable concentration of Vydate (see below), a trial was conducted to ascertain the minimum time required to kill stream invertebrates without having detrimental effects on algae as indicated by the percent phaeopigments to total pigment concentration. Samples were set up as previously described except that a 5 ppm solution of Vydate was used in all trials. Five cobbles were placed in this solution for increasing lengths of time (4, 8, 12, 24 h), after which algal pigment concentrations were measured. Cobbles placed in river water alone for 24 h acted as controls. Invertebrates were also exposed to a 5 ppm concentration of Vydate and the number of individuals alive at each time interval was recorded. The numbers of larvae used in trials was the same as in the earlier experiment.

RESULTS

Effect of Vydate concentration

Increasing concentrations of Vydate caused significant increases in the percentage of phaeopigments extracted from periphyton on cobbles ($F= 18.6$, $p<0.001$; Fig 1) indicating some cellular damage at higher Vydate concentrations.

Invertebrates present in river water experienced least mortality, with Deleatidium larvae having the highest mortality after 24 hours (six of the 30 larvae), and Limonia larvae having the least mortality (one of the 15 larvae). Exposure to

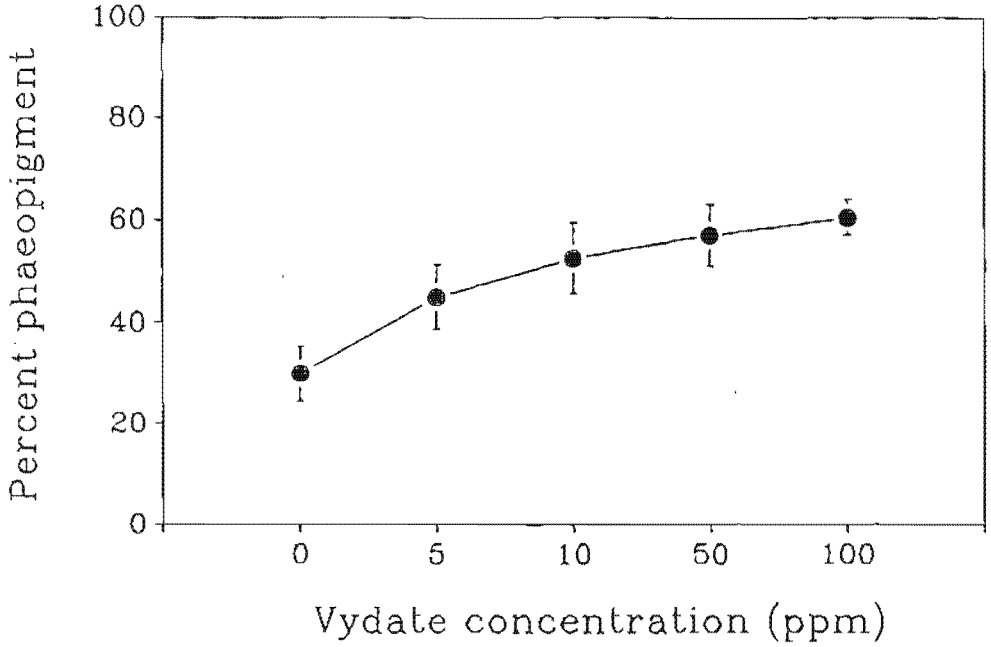


Fig. 1: Percentage phaeopigment to total pigment content extracted from natural periphyton immersed in increasing concentrations of Vydate for 24 h.

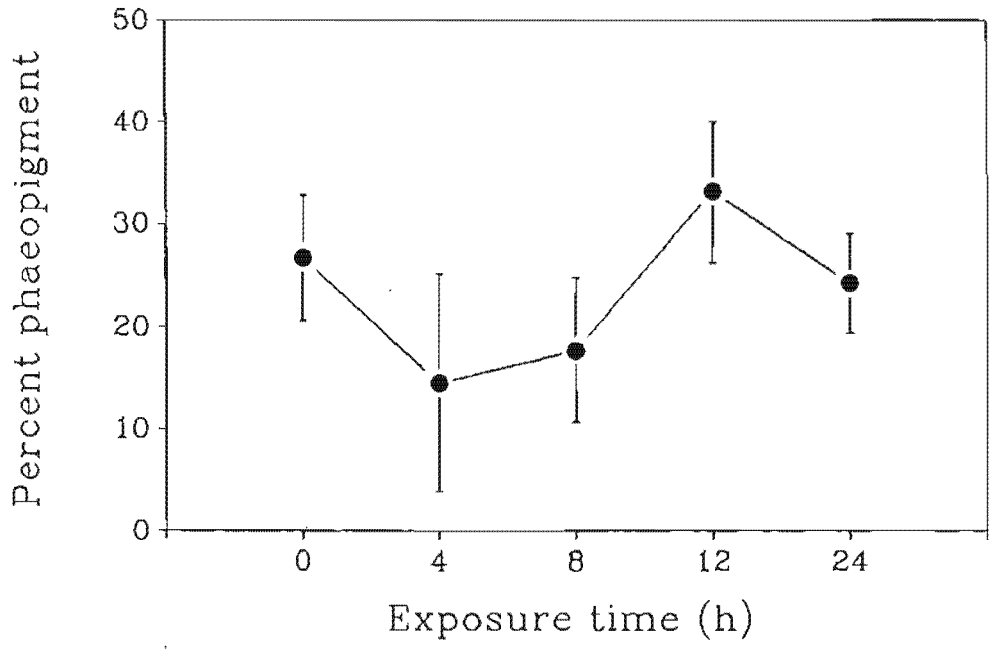


Fig. 2: Percentage phaeopigment to total pigment content extracted from natural periphyton immersed in a 5 ppm solution of Vydate for increased lengths of time.

5 ppm Vydate (24 h) resulted in complete mortality of Chironomidae and *Hydroblosis* larvae, whereas this concentration killed only 6 of the twelve *Olinga feredayi* larvae. Exposure to concentrations of 10 ppm and above resulted in 100% mortality of all invertebrates.

Effect of time

Although the 10ppm concentration of Vydate was the minimum required to obtain 100% mortality of all taxa, some cellular damage to algae was suggested by the increase in the percentage of phaeopigments to total pigments. To minimise any possible damage to algal communities on artificial mosses I decided to use Vydate at a concentration of 5 ppm as this concentration of Vydate resulted in the lowest increase in the ratio of phaeopigments to total pigments.

Immersion of periphyton communities in a 5 ppm Vydate solution resulted in no changes in phaeopigment:total pigment ratio ($F= 1.62$, $p>0.05$; Fig 2). Mortality of invertebrates increased as the time exposed to 5 ppm Vydate increased (Fig 3). Different taxa displayed markedly different sensitivities to Vydate over time: all chironomid larvae died after 4 hours but 20% of *Limonia* larvae were still alive after 12 hours. After 8 hours larvae of *Limonia*, *Deleatidium*, and *Zelandoperla* were obviously affected by the chemical. They showed strong muscular contractions and lay quivering at the bottom of each container. Mortality of all test species except *Limonia* was complete after 12 hours exposure, and all the latter were clearly affected by the chemical.

DISCUSSION

The use of Vydate at a concentration of 5ppm for 12 hours killed most invertebrates tested but had little effect on algal communities. Although only insect taxa were used in my tests, Vydate has a known lethal concentration (LC_{50}) toxicity (48 h exposure) of only 1.95 ppm for *Daphnia magna* (Manufacturers User Guide). Thus, 5 ppm Vydate was likely to have also killed crustacean taxa targeted for removal from artificial substrata.

Vydate has strong anti-cholinesterase activity which results in severe, uncontrolled muscular contractions. These were observed in test animals exposed to the 5 ppm solution for 2 hours or more. As artificial mosses were suspended upside down in containers of the solution, I expected that animals would first fall away from the substrata as they became irritated and muscular contractions commenced. This was indeed the case and after a 12 h exposure period, most dead animals were on the bottom of the containers.

Dead animals that remained amongst the strands of artificial bryophytes were assumed to have been washed away when substrata were returned to the

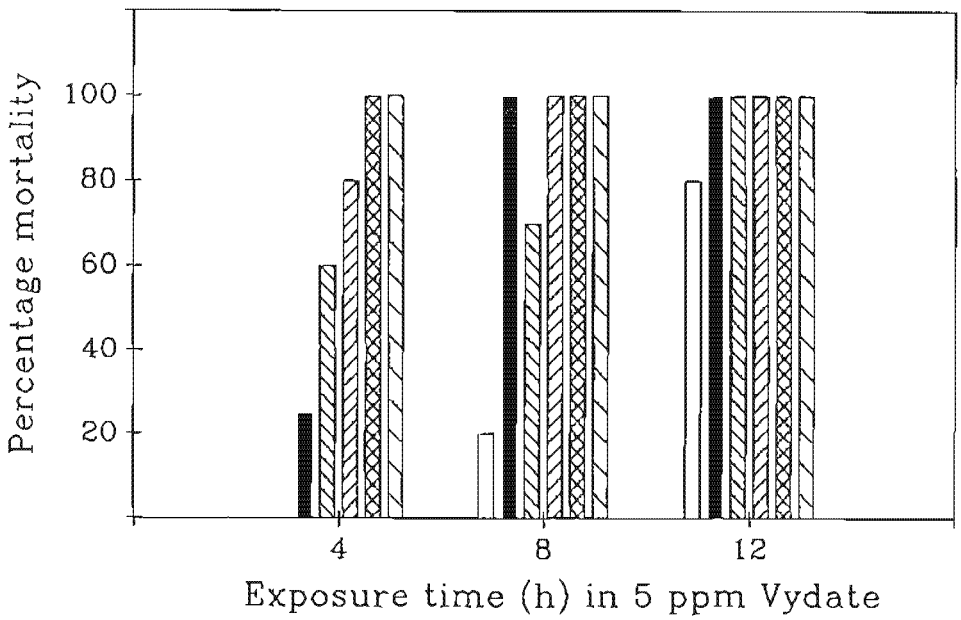


Fig. 3: Percentage mortality of various invertebrate taxa exposed to a 5 ppm solution of Vydate for increased lengths of time. open bars = *Limonia hudsoni;* closed bars = *Hydroblosis* sp.; narrow right-hand crossed bars = *Zelandoperla* sp.; narrow left-hand crossed bars = *Deleatidium* sp.; crossed hatched bars = Chironomidae; wide right-hand bars = *Olinga feredayi.*

stream in field experiments. The rapid (12 h) photo-oxidation of Vydate into harmless by-products, and the constant washing by stream water would have ensured that chemical treatment did not affect subsequent colonization of substrata by animals.

Since Vydate removed a wide range of invertebrate taxa from artificial substrata without apparently harming natural periphytic communities, I was able to examine the rates of invertebrate colonization with and without the presence of algae on substrata placed in two small alpine streams (Chapter 5).

APPENDIX FOUR:

THE ECOLOGICAL ROLE OF BRYOPHYTES

IN HIGH ALPINE STREAMS OF NEW ZEALAND

Verh. Internat. Verein. Limnol.	23	1412–1416	Stuttgart, Oktober 1988

The ecological role of bryophytes in high alpine streams of New Zealand

A. M. Suren

With 8 figures in the text

Introduction

Aquatic bryophytes can be abundant in small New Zealand alpine streams where they sometimes cover large areas of substratum. Despite their small size, bryophytes alter stream microenvironments as do macrophytes (Gregg & Rose 1985) and so may be expected to influence macroinvertebrate distribution. Bryophytes are used by animals for shelter during floods (Maurer & Brusven 1983), for oviposition (Byers 1961, Gerson 1972), for protection during pupation (Cowley 1978) and to hide from predators (Glime 1978).

Few studies have examined the faunas associated with bryophytes (Glime 1968, Cowie & Winterbourn 1979) or compared faunas on bare stones and bryophyte covered substrata (Percival & Whitehead 1929, Maurer & Brusven 1983). Mosses may not be important to animals per se but they may act as a surface for periphyton growth and detrital accumulation, and consequently attract invertebrates (Glime & Clemons 1972). Although some animals feed on bryophytes (Mutch & Pritchard 1984), this generally is not the rule (Frankland 1974).

The aims of the present study are to compare the invertebrate faunas in mossy and non-mossy areas of two alpine streams and to determine how bryophytes are used by aquatic invertebrates.

Study sites

Two study sites were chosen in Arthur's Pass National Park (Lat 43° 57', Long 171° 34'), South Island, New Zealand. Site 1, named "Mouse Stream", is a small stream above the tree line that flows off Goldney Ridge into the Otira River. It is surrounded by dense riparian vegetation consisting of alpine tussock (*Chionochloa* sp.), giant buttercups (*Ranunculus lyallii*) and mountain hebe (*Hebe subalpina*). The dominant bryophytes are the mosses *Fissidens rigidulus*, *Cratoneuropsis relaxa* and *Bryum blandum*. Site 2, called "Tim's Creek", flows through a mountain beech forest (*Nothofagus solandri* var. *cliffortioides*) on the lower slopes of Mt. Cassidy. Other riparian plants here are tussock grasses, small hebes and ferns. The dominant bryophytes are the liverworts *Plagiochila retrospectans* and *Lophocolea planiuscula* and the mosses *F. rigidulus* and *Pterygophyllum dentatum*. The stream beds at both sites consist of bedrock and a mixture of cobbles, gravels and fine sand with bryophytes occurring only on the bedrock and large cobbles.

Materials and methods

Mossy areas were sampled with a 0.01 m² Surber sampler (100 µm mesh) into which mosses were scraped with a razor blade. Rocky areas were sampled with a second Surber sampler (area = 0.02 m², 100 µm mesh) which had a thick foam flange around its bottom to ensure a proper seal with the substratum. Sampling was conducted monthly for six months (July to December), with five replicates being taken from each habitat at each site. Samples were frozen and later thawed, sorted on nested sieves (250 µm, 500 µm, 1.0 mm and 2.0 mm) and invertebrates identified and counted under a binocular microscope.

Artificial "mosses" were constructed by weaving pieces of nylon twine (5 cm long, 1 mm thick) into squares (0.01 m²) of firm nylon mesh (pore size 4 mm). In October, five replicate "mosses"

0368-0770/88/0023-1412 $ 1.25

were placed in areas at both sites from which moss samples had been taken previously. They were sampled 2 months later in December which allowed detritus and periphyton to establish.

Scanning electron microscopy was used to observe periphyton growing on living bryophytes and artificial mosses, to examine the accumulation of detritus on artificial mosses, and to look for evidence of grazing or other kinds of bryophyte utilization by invertebrates. Samples for SEM observations were fixed in 2% gluteraldehyde in phosphate buffer (pH = 7.5) and dehydrated as per NEUMANN et al. (1982).

Results and discussion

Distribution and abundance of invertebrates

Distinct animal assemblages were found in both rocky and mossy habitats at both sites. Dominant bryophilous animals were the stonefly larvae *Zelandoperla* and *Zelandobius*, Chironomidae, Dorylaimoidea (Nematoda), Oribatei and Hydracarina (Acarina), Copepoda and Ostracoda. The mayfly larvae *Deleatidium* and *Nesameletus* were most abundant in rocky areas. With the exception of Tardigrada, which occurred exclusively at Mouse Stream, and of *Orchymontia calcarata* and *Homalaena ?dispersa* (Hydraenidae: Coleoptera) which were characteristic of Tim's Creek, animal communities at both sites were similar.

Significant differences in total densities of animals were found between the two sites (1-Way ANOVA, $F = 126.83$, $p < 0.01$) with Mouse Stream supporting about 5 times as many animals per unit area than Tim's Creek. Significant differences in animal abundance were found also between mossy and rocky areas at each site ($F = 144.70$, $p < 0.01$). Mossy habitats supported 5—15 times more invertebrates than rocky areas (Figs. 1 and 2). This is very similar to results obtained by MAURER & BRUSVEN (1985) who found that *Fontinalis neomexicana* supported 5—30 times more insects than mineral substrata.

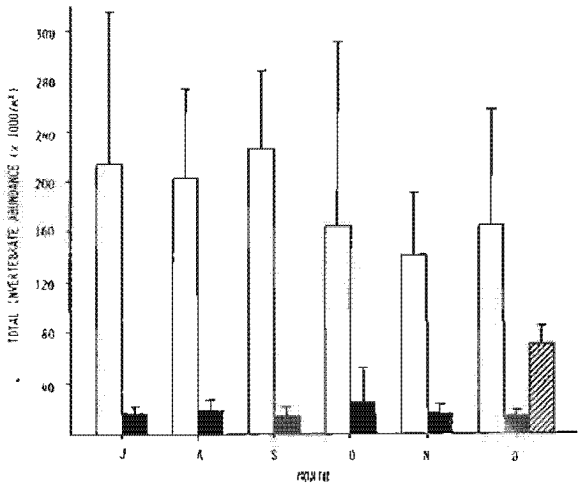


Fig. 1. Total numbers of invertebrates collected from mossy habitats (open bars) and rocky habitats (shaded bars) at Mouse Stream (x +/− 2 SE, n = 5). Striped bar represents abundance of animals collected from artificial mosses.

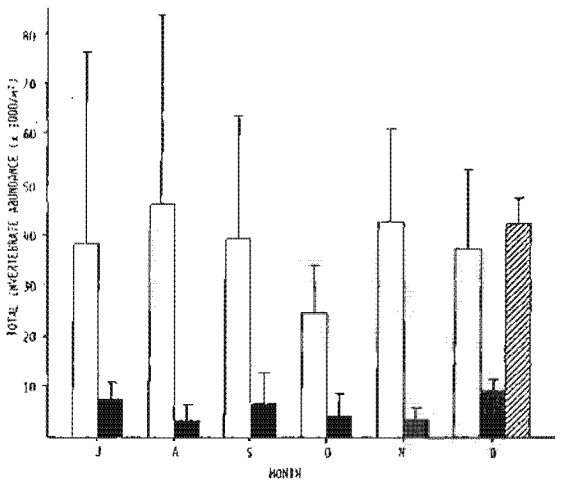


Fig. 2. Total numbers of invertebrates collected from mossy habitats (open bars) and rocky habitats (shaded bars) at Tim's Creek (x +/− 2SE, n = 5). Striped bar represents abundance of animals collected from artificial mosses.

Artificial moss fauna

The faunas colonizing artificial mosses were similar to those on living bryophytes. Significantly more animals occurred on artificial mosses than rocky areas at both sites ($t = 7.58$ for Mouse Stream, $t = 11.2$ for Tim's Creek, $p < 0.01$), but no significant differences were found between artificial and real mosses ($t = 1.98$ for Mouse Stream, $t = 0.62$ for Tim's Creek, $p > 0.05$) (Figs. 1 and 2). Certain taxa, however, were present in significantly lower numbers on artificial mosses than on real bryophytes (unpublished data). These included Acarina, Collembola, Tardigrada, Dorylaimoidea and Ostracoda.

If the microenvironment among artificial and real mosses is similar, then the main difference between them is likely to be the inedibility of the artifcial mosses. Overall faunal similarities between these two habitats suggest that few bryophyte dwelling insects use them as food. This supports the contention of Glime & Clemons (1972) that mosses serve only as a substratum for invertebrates. The reduction in numbers of certain non-insect taxa on artificial mosses suggests, however, that some animals may be dependent upon bryophytes for food.

SEM observations

In winter, only a sparse periphyton consisting of bacilli, actinomycetes and trapped detrital particles occurred on bryophytes in Mouse Stream. With increasing day length and water temperatures in spring, large algal blooms developed on both rocks and bryophytes. This periphyton consisted chiefly of flocculent masses of *Diatoma* sp. (Bacillariophyceae) and *Ulothrix* sp. (Chlorophyta), clumps of a cyanophyte (probably *Placoma* sp.) and tufts of *Tolypothrix* sp. and *Chamaesiphon* sp. (Cyanophyta). Increases in algal biomass increased the quantities of potentially available food in both habitats at Mouse Stream but this had no apparent effect on animal abundance. Algal growth at

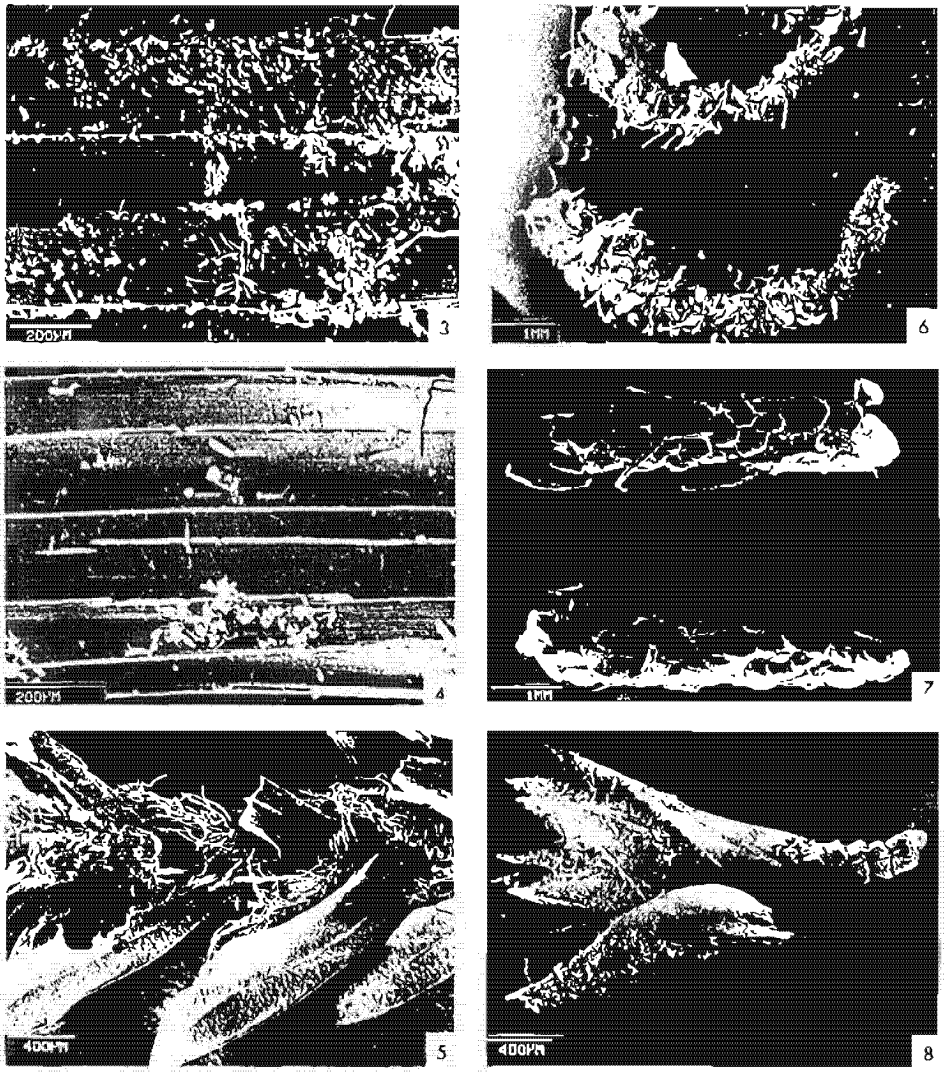


Fig. 3. Abundant periphyton growth on artificial mosses from Mouse Stream.
Fig. 4. Sparse accumulations of detritus and silt on artificial mosses from Tim's Creek.
Fig. 5. *Fissidens rigidulus* from Mouse Stream showing evidence of invertebrate biting.
Fig. 6. Case construction utilizing bryophytes by Chironomidae larvae.
Fig. 7. *Zelolessica* sp. larvae often construct portable retreats solely from bryophyte tissue.
Fig. 8. Pupating chironomid sheltering in apical leaves of *Cratoneuropsis relaxa*.

Tim's Creek was negligible during winter and spring, and consisted mainly of the encrusting diatom *Epithemia* sp. (Bacillariophyceae).

Artificial mosses placed in Mouse Stream in summer were also covered with abundant periphyton (Fig. 3), but at Tim's Creek they mainly collected detritus and silt (Fig. 4). SEM observations also showed that bryophyte tissue was grazed at both sites (Fig. 5). Re-

treat dwelling insect larvae such as some Chironomidae and *Zelolessica* sp. (Trichoptera) utilized bryophyte material for case construction (Figs. 6 and 7), and pupating chironomids were found within bryophyte shelters (Fig. 8). Pieces of living bryophyte material were also found occasionally in guts of oeconesid caddisfly larvae (*Oeconesus maori* and *Zelandopsyche ingens*), larval Empididae and Muscidae (Diptera), Dorylaimoidea (Nematoda) and Tardigrada (unpublished data).

In the two alpine streams studied, bryophytes create a microhabitat that provides shelter for aquatic invertebrates, a site for periphyton growth and the accumulation of detritus, potential foods and material for case construction by larval insects. While replacement of real bryophytes with artificial structures resulted in the redevelopment of similar animal communities, some taxa (Acarina, Collembola, Tardigrada, Dorylaimoidea, and Ostracoda) appeared to be negatively affected by the loss of a bryophyte food source.

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References

Byers, G. W., 1961: The crane fly genus *Dolichopeza* in North America. — *Kansas Univ. Sci. Bull.* 42: 655—924.

Cowie, B. & Winterbourn, M. J., 1979: Biota of a subalpine springbrook in the Southern Alps. — *N. Z. J. Mar. Freshwat. Res.* 13: 295—301.

Cowley, D. R., 1978: Studies on the larvae of New Zealand Trichoptera. — *N. Z. J. Zool.* 5: 639—750.

Frankland, J. C., 1974: Decomposition of lower plants. — In: *Biology of plant litter decomposition* 1: 3—36, eds. C. H. Dickinson & G. J. F. Pugh. Academic Press, London.

Gerson, U., 1972: Bryophytes and invertebrates. — In: *Bryophyte ecology*, Chapter 9: 291—332, ed. A. J. E. Smith. Chapman and Hall, London.

Glime, J. M., 1968: Insect communities among Appalachian mountain stream bryophytes. — PhD. Thesis, Michigan State Univ., 180 pp.

— 1978: Insect utilization of bryophytes. — *Bryologist* 81: 186—187.

Glime, J. M. & Clemons, R. M., 1972: Species diversity of stream insects on *Fontinalis* spp. compared to diversity on artificial substrates. — *Ecology* 53: 456—464.

Gregg, W. W. & Rose, F. L., 1985: The effects of aquatic macrophytes on the stream microenvironment. — *Aquat. Bot.* 14: 309—324.

Maurer, M. A. & Brusven, M. A., 1983: Insect abundance and colonization rate in *Fontinalis neomexicana* (Bryophyta) in an Idaho batholith stream, U. S. A. — *Hydrobiologia* 98: 9—15.

Mutch, R. A. & Pritchard, G., 1984: The life history of *Zapada columbiana* (Plecoptera: Nemouridae) in a rocky mountain stream. — *Can. J. Zool.* 62: 1273—1281.

Neumann, A. J., Rushing, A. E. & Mueller, D. M. J., 1982: A modified, short protocol for preparation of bryophytes for scanning electron microscopy. — *Bryologist* 85: 74—79.

Percival, E. & Whitehead, H., 1929: A quantitative study of the fauna of some types of stream bed. —*J. Ecol.* 17: 282—314.

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